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Conservation Biology of Elasmobranchs

Steven Branstetter (editor)

U.S. Department of Commerce

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U.S. DEPARTMENT OF COMMERCE
Ronald H. Brown, Secretary
National Oceanic and Atmospheric Administration
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National Marine Fisheries Service

Contents

Introduction

Elasmobranchs are vital and valuable components of the marine biota. From an ecological perspective they occupy the role of top predators within marine food webs, providing a regulatory control that helps balance the ecosystem. From an evolutionary perspective, this group represents an early divergence along the vertebrate line that produced many unusual, but highly successful, adaptations in function and form.

From man's perspective, elasmobranchs have been considered both an unavoidable nuisance, and an exploitable fishery resource. A few of the large shark species have earned a dubious notoriety because of sporadic attacks on humans that occur in coastal areas each year worldwide; the hysteria surrounding an encounter with a shark can be costly to the tourist industry. More importantly, elasmobranchs are often considered a detriment to commercial fishing operations; they cause significant economic damage to catches and fishing gear. On the other hand, consumer attitudes have changed concerning many previously unpopular food fishes, including elasmobranchs, and this group of fishes has been increasingly used by both recreational and commercial fishing interests. Many elasmobranchs have become a popular target of recreational fishermen for food and sport because of their abundance, size, and availability in coastal waters. Similarly, commercial fisheries for elasmobranchs have developed or expanded from an increased demand for elasmobranch food products.

Unfortunately, elasmobranch stock-recruitment relationships are generally density-dependent, and their innate biological characteristics of slow growth, late maturation, and low fecundity do not support extensive exploitation. Today, many elasmobranch populations, and stocks, are jeopardized by overexploitation, and substantially reduced populations will have long-term negative impacts, not only for the elasmobranch stocks (and human user-groups), but to the marine community of which they are a part. There are numerous examples of imbalances that have occurred within communities after the primary apex predators were removed or reduced.

This was the third symposium convened in less than four years designed to elucidate the status of elasmobranch resources worldwide. Twenty-four authors contributed 16 formal and two informal presentations on a variety of topics concerning elasmobranch biology, use, management, and conservation. Nine of the 16 formal oral presentations translated into eight manuscripts for the proceedings of this symposium. Three presentations were slated for publication elsewhere, and four authors considered their results too preliminary to warrant publication at this time. In addition, this volume contains one paper by Sandra Zeiner that was a co-winner of the 1991 American Elasmobranch Society *Gruber Award* for the best student presentation.

The development of the symposium was possible only with the help of Sandra Zeiner and Jefferey Howe of the Symposium Committee. I would like to thank Michael Smith (Chair, Local Organizing Committee, the American Society of Ichthyologists and Herpetologists) and the host institution (The American Museum of Natural History, New York) for their support. I want to extend a special note of appreciation to Harold (Wes) Pratt Jr. (Chair, Local Organizing Committee, the American Elasmobranch Society) for his many hours of help in coordinating the symposium as part of the AES meeting. I congratulate the session chairs — John Morrissey, Robert Hueter, and Jefferey Howe — for keeping the ever-changing program on schedule. Each article was peer-reviewed by at least two anonymous referees consisting of symposium participants and 'outside' experts. Overall, 21 individuals contributed comments that improved the quality of these manuscripts; their expertise is greatly appreciated. Finally, I wish to thank the authors and symposium participants. These contributions will benefit man's efforts to understand and ultimately conserve this important marine resource.

Steven Branstetter, Editor
Gulf and South Atlantic Fisheries
Development Foundation
Tampa, Florida, 1993

Trends in Shark Abundance from 1974 to 1991 for the Chesapeake Bight Region of the U.S. Mid-Atlantic Coast*

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ABSTRACT

Recent stock assessments indicate that the shark stock of the western North Atlantic is exploited at a rate twice the maximum sustainable yield. This finding is supported by data generated by the Virginia Institute of Marine Science longline program for sharks of the Chesapeake Bay and adjacent coastal waters. Trends in catch per unit of effort since 1974 indicate 60–80% reductions in population size for the common species — sandbar (*Carcharhinus plumbeus*), dusky (*C. obscurus*), sand tiger (*Odontaspis taurus*), and tiger (*Galeocerdo cuvier*) sharks. Declines include numbers of individuals for all species, size classes within species, and in one case a strong decline in relative abundance. Given the limited ability of sharks to increase their population size, these results suggest that stock recovery will probably require decades.

Introduction

The sharks of the northwest Atlantic have been increasingly exploited by recreational and commercial fisheries over the last 20 years. Because many of the species are highly migratory (Casey and Kohler, 1990), they are available to numerous regional fisheries on the U.S. east coast, and in some instances, to fisheries in Cuba, Mexico, and other Latin American countries (Springer, 1979; Anderson, 1990a; Bonfil et al., 1990). Thus there is wide-scale fishing pressure on the populations.

U.S. interest in recreational shark fishing rose in the mid-1970's following the release of the movie "Jaws"; shark fishing clubs and tournaments expanded throughout the region (Casey and Hoey, 1985; Hueter[1]). Additionally, apparent declines in abundance of traditional teleost target species like tuna, marlin, and snapper led many charter and head boat captains to fish for sharks to satisfy clients (NMFS[2]). Recreational catches are estimated at 2.5 million sharks annually, or 35,000 metric tons; annual mortality associated with this catch may exceed 10,000 t (Hoff and Musick, 1990).

Commercial use of sharks has been sporadic and based on economic parameters of supply and demand. Based on the success of a 1940's Florida-based fishery for shark liver oils (Springer and French, 1944; Springer, 1949, 1951), shark fishing was later promoted as a control measure against the economic damages sharks caused to other fishing operations and to the tourist service industry (Springer and Gilbert, 1963; Beaumariage, 1968). However, although sharks were a major bycatch in various fisheries (Cody et al., 1981; Anderson, 1985, 1990a, 1990b; Berkeley and Campos, 1988), the catch was usually discarded because of its

*VIMS Contribution No. 1782

[1] Hueter. R. E. 1991.—Survey of the Florida recreational shark fishery utilizing shark tournament data and selected longline data. Final Report to Fla. Dept. Natl. Resources, Grant #6627, 74 p.

[2] National Marine Fisheries Service (NMFS). 1991. Draft (19 April 1991) Secretarial Shark fishery management plan for the Atlantic Ocean. U.S. Dep. Commer. NOAA, Nat. Mar. Fish. Serv., Southeast Regional Center, St. Petersburg, FL, 127 p.

low ex-vessel value and because of limited onboard storage capability. Only easily stored shark products with market value, such as jaws and fins, were sold by vessel crews as supplemental income.

This shark discard was identified as an underutilized resource with a potential for fishery expansion (Ronsivalli, 1978; Springer, 1979; Colvocoresses and Musick, 1980; Branstetter, 1981a; Cody et al., 1981; Stevens et al., 1982; Cook, 1982; Cook (ed.), 1987; Berkeley and Campos, 1988). Shark meat was recognized as a high-protein, low-fat food source (Gordievskaya, 1971) containing high quantities of lysine, an amino acid important in fish meal (Kreuzer and Ahmed, 1978). Driven by an increasing price for fins, shark landings increased from fisheries that took a large shark bycatch (Graham, 1987; Berkeley and Campos, 1988). As more shark was landed, a supportive market developed on both a domestic and international level, and more vessels shifted their directed efforts toward shark. Shark landings rose exponentially after 1985, totalling > 7100 t in 1989 (NMFS[2]).

In addition to rising U.S. landings, established commercial fisheries for sharks have expanded throughout the Caribbean and southern Gulf of Mexico (Kleign 1974; Springer, 1979; Bonfil et al., 1990). In recent years, foreign squid and tuna fleets have also taken a substantial bycatch of sharks from their efforts in the region (Anderson, 1985, 1990a; Witzell, 1985).

Shark mortality within FAO Area 31 (the U.S. mid-Atlantic and Caribbean region) has been estimated to exceed 42,000 t whole weight; 22,000 t of which was from U.S. waters (Anderson, 1990a). This mortality level exceeds the 9,800–16,500 t whole weight maximum sustainable yield (MSY) estimated for U.S. waters (Anderson, 1990b; Parrack, 1990); thus the stock is apparently overexploited. Sharks are particularly vulnerable to overfishing because of their slow growth, late maturation, and low fecundity (Holden, 1974, 1977). Historically, shark fisheries have succumbed, owing in part, to overfishing (Byers, 1940; Ripley, 1946; Olsen, 1959, 1984; Springer, 1951; Aasen, 1963; Grant et al., 1979; Thorson, 1982; Cailliet and Bedford, 1983; Florida Sea Grant, 1985; Holts, 1988; Smith and Abramson, 1990).

Hoff and Musick (1990) noted that strict management was needed for conservation and rational long-term utilization of the shark stocks in the northwest Atlantic because of the limited ability of the stocks to withstand heavy fishing pressure. A federal shark fishery management plan for the U.S. east coast is in preparation (NMFS[2]); in the interim, several states have enacted laws to regulate shark fisheries within their respective waters (14% of commercial and 64% of recreational catches occur in state controlled waters [NMFS[2]]). Hoff and Musick (1990) also noted the dearth of appropriate data available for stock assessments, and Parrack (1990) indicated that the lack of these data hindered his assessment for the management plan. This information included

- biological data (delineation of nursery grounds, age structure, reproduction, stock delineation),
- species-specific fisheries data (catch/effort, size and weight data), and
- fishery-independent assessment.

Such data are crucial to adequately derive projections of maximum sustainable yield on a species-by-species basis.

To that end, the Virginia Institute of Marine Science (VIMS) has conducted a longline sampling program since 1974 examining the distribution, abundance, and biology of sharks and large pelagic teleosts off Virginia. This long-term program provides information on the three data needs listed above. This report analyzes trends in catch, effort, and species composition from 1974 through 1991 for the Chesapeake Bight region, and highlights pertinent biological features associated with these data.

Methods and Materials

Sharks were collected by longlines fished from May through October 1974–1991. The majority of longlines were fished at specific stations from the lower Chesapeake Bay to the edge of the continental shelf (200-m contour). For analysis, these stations were stratified by depth: 1) lower Chesapeake Bay; 2) coastal (<10 m depth); 3) nearshore (10–20 m depth); 4) mid-shelf (20–100 m depth); and 5) offshore (>100 m depth). Supplemental localities within these strata were fished on occasion to provide additional data on species distributions within strata.

A longline consisted of a 6.4-mm (1/4") hard-laid and tarred nylon mainline anchored at both ends with 3–5 m gangions spaced about 20 m apart and set with buoys at 20-gangion intervals. Gangions were composed of a heavy-duty quick-snap with 8/0 swivel, 2–3 m of 3 mm (1/8") hard-laid and tarred nylon line, an 8/0 swivel connecting 1–2 m of 1.6 mm (1/16") 1X7 or 7X7 stainless steel wire, and a 9/0 hook. Based on sonar scans of longlines set in deep water, the catenary of the mainline reached depths exceeding 80 m; thus, for most coastal stations the majority of hooks were on or near the bottom specifically targeting semi-demersal species. Soak time varied from 2 to 17 hr, but most sets were of 3–4 hr duration. Bait varied with local availability but consisted primarily of coastal teleost fishes such as croaker, spot, menhaden, bluefish, and mackerel. Bait pieces were 0.10–0.25 kg each in order not to

exclude the capture of small fish. A standard 100 hook longline covered about 2 km (1.25 miles).

Complete records were kept for each set. Data included 1) location; 2) start and finish times for set and haul operations; 3) water depth; 4) water temperatures at the surface and bottom (to a maximum of 30 m); 5) number of hooks; and 6) bait type. Each shark caught was identified to species; measured for pre-caudal length (PCL), fork length (FL), and total length (TL) to the nearest cm; weighed (lbs.); and sexed. Pertinent biological data and samples were collected. Healthy sharks not needed for biological sampling were tagged with M-type dart tags supplied by the National Marine Fisheries Service and released after species, length, and sex were determined; lengths were estimated for those large sharks that could not be safely boarded. Sharks that broke the gangion or dislodged the hook after being brought alongside were counted as a catch, and noted as a "lost" shark. Broken gangions, or 'bite-offs,' retrieved during haul-back, were not recorded as a lost shark.

Yearly fishing efforts varied with programmatic support and immediate research goals (Table 1). During 1980 and 1981, stations were surveyed on a monthly basis from May through October; 1990 and 1991 efforts replicated the 1980–81 effort, in addition to sampling ancillary localities. However, some years were represented by as little as 200–500 hooks of effort. Sampling within a depth stratum was sometimes confined to a single month which provided limited information on the spatial and temporal distributions of species over an entire year (Table 2). Sampling months varied among years, and some depth strata were sampled disproportionately. Additionally, shifting prioritites during the 1980's led to efforts over a wider geographic range, from Washington Canyon in the north to Cape Hatteras in the south. Ancillary localities of similar habitat were sometimes fished in lieu of established stations, and offshore (>100 m) sampling was greater than 1/3 of the total effort during this period (Fig. 1).

Sampling was directed at biological and ecological objectives; fishery analysis was not an a priori objective of the sampling program. Even when effort is evenly distributed, longlining as a sampling method is notorious for its variable catch rates (Branstetter, 1981a; Berkeley and Campos, 1988). Combined with changing programmatic goals and sampling effort, these variations precluded the use of standard statistical procedures. Large sample sizes that would reduce such variability were not always available in this data base (Table 1; Table 2); thus, graphically-apparent trends between consecutive years were not always significantly different. Yoccoz (1991) emphasized that statistical significance, or lack thereof, does not equate with biological significance, and that biological significance levels should be set before sampling begins. For this reason, this presentation is restricted to analysis of trends over the 18-yr period. For illustrative purposes, low-effort years were combined into multi-year categories by grouping 1974–79 and 1982–89. Although combining data from consecutive years reduced the information available for a given year, it provided a more equitable basis of effort to illustrate the long-term continuum in catch and effort trends around the comprehensive high-effort survey periods 1980–1981 and 1990–1991.

Catch per unit of effort (CPUE) was defined as the total number of sharks caught for the total number of hooks fished, multiplied by 100 within each sampling category, although the number of hooks per set increased over time (Table 1). CPUE was analyzed for total catch and by individual species in designated year categories. Because sharks segregate by sex and size, disjunctly distributed by depth on a seasonal basis, CPUE was analyzed for each time-series by depth strata and by month. The majority of species considered were coastal sharks; thus, because of the relatively higher percentage of hooks fished in offshore (>100 m) waters during the 1980's and in 1990 (Fig. 1, D–E), species-specific CPUE analyses were restricted to efforts from the Bay to the 100-m depth contour to avoid negatively biasing results for these species. Efforts in the >100-m depth category were included only for total CPUE and CPUE for the more widely distributed dusky and scalloped hammerhead sharks. Additionally, after 1981, new sampling areas — offshore (>100 m) areas away from the standard station at Norfolk Canyon, and a lagoon within the Virginia eastern shore peninsula — were fished for very specific purposes. These efforts (Fig. 1, D–F) were not directly comparable with previous data, and were excluded from analyses.

Results

A total of 383 sets, comprising of 33,115 hooks, caught 2,736 sharks of 20 species. Based on categorization of data and exclusion of extraneous efforts, this report (Table 1) includes 329 sets, totalling 28,329 hooks, that caught 2346 sharks of 20 species (Table 3). Analyses are provided for six species taken consistantly throughout the survey period. Other species, some of which were taken in good numbers, occurred only sporadically over time; thus they were excluded from further analyses.

Relative Abundance

Species composition remained relatively stable throughout the survey (Fig. 2); however, the numbers of individuals collected declined strongly over the survey period even though effort generally increased. The sandbar shark (*Carcharhinus plumbeus*) was the dominant

Table 1

Catch and effort data of VIMS longline program for 1974-1991 used for analysis. Sampling localities were categorized by depth strata. Numbers in parentheses in the ">100 m" category are additional sets not included in analyses, but indicate the inshore-to-offshore shift in research priority of the VIMS longline program over time. To provide more equitable amounts of effort for comparison, the years 1974–1979 and 1982–1989 were combined. An intermediate grouping of year categories — 1974–76, 1977–1979, 1982–85, 1986–89 - is provided for comparative purposes. Catch per unit of effort (CPUE) equals sharks per 100 hooks.

	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991
BAY																		
Sharks	23	44	15	36		4	102	57	1							12	122	112
Hooks	162	198	38	228		120	1200	500	50							200	1476	740
No. sets	4	5	1	3		2	12	5	1							2	16	8
<10 m																		
Sharks	34	47	25	68	29	5	277	243	5	7	7		1	33	11	1	51	41
Hooks	181	286	106	595	180	60	1900	1700	96	259	208		75	184	72	97	1347	1045
No. sets	4	7	3	9	3	1	19	17	1	3	3		1	3	1	1	16	11
10–20 m																		
Sharks	15	29		6	9		136	145		23	7	2	3	7	9	12	75	59
Hooks	142	119		62	56		700	1100		261	79	70	172	96	105	187	1200	1095
No. sets	3	3		1	1		7	11		3	1	1	2	1	1	2	12	11
20-100 m																		
Sharks	10	26	16	6		2	55	65	43	13	2		2	13	5	6	41	49
Hooks	74	136	68	215		41	500	500	190	272	81		86	200	190	180	1043	2170
No. sets	2	4	2	3		1	5	5	2	3	1		1	2	2	2	10	22
>100 m																		
Sharks			6			17	10	22	4	3	18	4	1	3	1	0	3	3
Hooks			36			200	350	350	192	91	219	150	241	194	200	102	770	550
No. sets			1(1)			2	4	4	2	1(2)	3(1)	2(3)	3(1)	2(1)	2(3)	1	7(9)	6(2)
TOTAL																		
Sharks	82	146	62	116	38	28	580	480	53	46	34	6	7	56	26	31	293	264
Hooks	559	739	248	1100	236	421	4650	4150	528	883	587	220	574	674	567	766	5827	5600
No. sets	13	19	7	16	4	6	47	42	6	10	8	3	7	8	6	8	61	58
Mean hooks/set	43	39	35	69	59	70	99	99	88	73	73	82	84	95	96	96	95	97
CPUE	14.7	19.8	25.0	10.5	16.1	6.7			10.0	5.2	5.8	2.7	1.2	8.3	4.6	4.1		
		18.8			10.4					6.3				4.7				
			14.3				12.5	11.6				5.4					5.0	4.7

Table 2

Monthly (May through October) distribution of effort by depth strata over the time period 1974— 1991. A plus (+) indicates a month surveyed, a dash (—) indicates no survey.

Region	1974 M J J A S O	1975 M J J A S O	1976 M J J A S O	1977 M J J A S O	1978 M J J A S O	1979 M J J A S O	1980 M J J A S O	1981 M J J A S O	1982 M J J A S O
Bay	– + – + + –	– – + – + –	– + – – – –	+ + + – – –	– – – – – –	+ + – – – –	+ + + + + +	– + + + + +	+ – – – – –
<10 m	+ – + + + –	+ + + + + +	– + + + – +	– – + + + +	– + – – – –	– – + – – –	+ + + + + +	+ + + + + +	– – – + – –
10–20 m	– + + – – +	+ – – – + +	– – – – – –	+ – – – – –	– + – – – –	– – – – – –	+ + + + + +	+ + + + + +	– – – – – –
20–100 m	– – – + + –	+ + + + – –	– + + – – –	+ + – + – –	– – – – – –	– – – – + –	+ + + + + –	– + + + + +	+ – – – – –
>100 m	– – – – – –	– – – – –	– – + – – –	– – – – – –	– – – – – –	– – – – + –	+ – + + – –	– + + – + +	– – – + – –

Region	1983 M J J A S O	1984 M J J A S O	1985 M J J A S O	1986 M J J A S O	1987 M J J A S O	1988 M J J A S O	1989 M J J A S O	1990 M J J A S O	1991 M J J A S O
Bay	– – – – – –	– – – – – –	– – – – – –	– – – – – –	– – – – – –	– – – – – –	– – – – + –	+ + + + + +	– + + + + –
<10 m	– – + + + –	– – + – + –	– – – – – –	– – – + – –	– + + – – –	– – + – – –	– – – – + –	+ + + + + +	+ + + + + –
10–20 m	– – – – + –	– + – – – –	– – + – – –	– – + + – –	– – – – + –	– – – – + –	– – – – + –	– + + + + +	+ + + + + –
20–100 m	– + + – – –	– – – + – –	– – – – – –	– – + – – –	– – + – + –	– – – – + –	– – – – + –	– + + + + +	+ + + + + –
>100 m	– – + – – –	– – + + + –	– – + – – –	– – + – – –	– – – – + –	– – – – + –	– – – – + –	– + + + + –	– – + + + –

species collected in the lower Chesapeake Bay and adjacent coastal regions, and constituted over 55% of the total catch. In contrast, relative abundance declined for the dusky shark (*Carcharhinus obscurus*). From 1974 through 1981 this species composed 10–20% of the total catch, and declined to approximately 5% of the total during 1982–1989. In 1990 only three individuals (1%) were collected; in 1991 only six (2%). This was in stark contrast to the 1980 catch of 117 dusky sharks.

Table 3

Numbers of individuals of 20 species of sharks collected on VIMS longlines from 1974 through 1991. Species are listed by order of abundance.

Species analyzed		
sandbar shark	*Carcharhinus plumbeus*	1293
Atlantic sharpnose shark	*Rhizoprionodon terraenovae*	352
dusky shark	*Carcharhinus obscurus*	243
sand tiger	*Odontaspis taurus*	113
tiger shark	*Galeocerdo cuvier*	53
scalloped hammerhead	*Sphyrna lewini*	38
Miscellaneous coastal species		
smooth dogfish	*Mustelus canis*	94
blacktip shark	*Carcharhinus limbatus*	56
spinner shark	*Carcharhinus brevipinna*	6
bull shark	*Carcharhinus leucas*	5
lemon shark	*Negaprion brevirostris*	5
spiny dogfish	*Squalus acanthias*	5
blacknose shark	*Carcharhinus acronotus*	1
Atlantic angel shark	*Squatina dumeril*	1
Miscellaneous oceanic species		
bignose shark	*Carcharhinus altimus*	37
silky shark	*Carcharhinus falciformis*	18
shortfin mako	*Isurus oxyrinchus*	15
blue shark	*Prionace glauca*	9
bigeye thresher	*Alopias superciliosus*	1
night shark	*Carcharhinus signatus*	1

Catch per Unit of Effort (CPUE)

CPUE for individual years (Fig. 3A) indicated an overall decline in shark abundance; however, fluctuations between consecutive years were often explainable as sampling biases associated with the months, location, and number of hooks fished during a given year. For example, the extremely low CPUE's for 1985 and 1986 were biased because of the large percentage of hooks fished in relatively unproductive offshore waters (Table 1). Reductions in variability were possible by combining three or four consecutive low-effort years into a single category (Fig. 3B); however, this eight-category method offered only slightly greater resolution of long-term trends than a six-category time-series (Fig. 3C). The six-category method is used here.

CPUE by Species

Total CPUE (Fig. 3C) was strongly affected by the dominance of the sandbar shark catch (Fig. 4A). Total CPUE and sandbar shark CPUE declined approximately two-thirds over the sampling period. For sandbar sharks, catches included neonates and large adults.

CPUE over time declined at varying rates for the other species. The strongest decline in CPUE was that of the dusky shark (Fig. 4B). This one-time common species in the Virginia region has only rarely been caught on longlines in recent years. The majority of individuals collected were juveniles. The sand tiger (*Odontaspis taurus*) and the tiger shark (*Galeocerdo cuvier*), were caught regularly, but in low numbers, on longlines. Catch rates for the sand tiger declined about 75% over

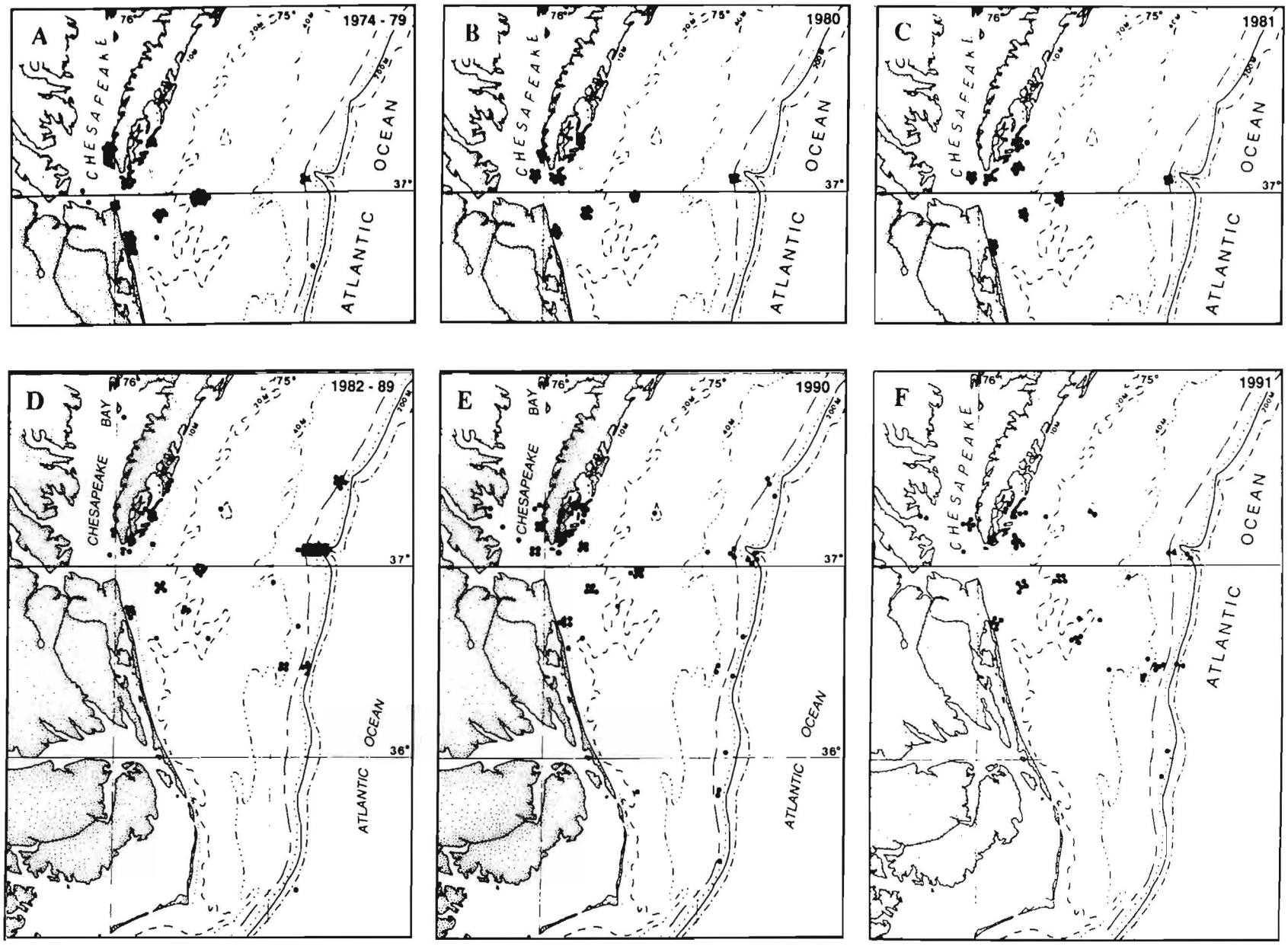

Figure 1

Location and number of all VIMS longline sets by year or year-group in the Chesapeake Bight of the mid-Atlantic coast of the United States.

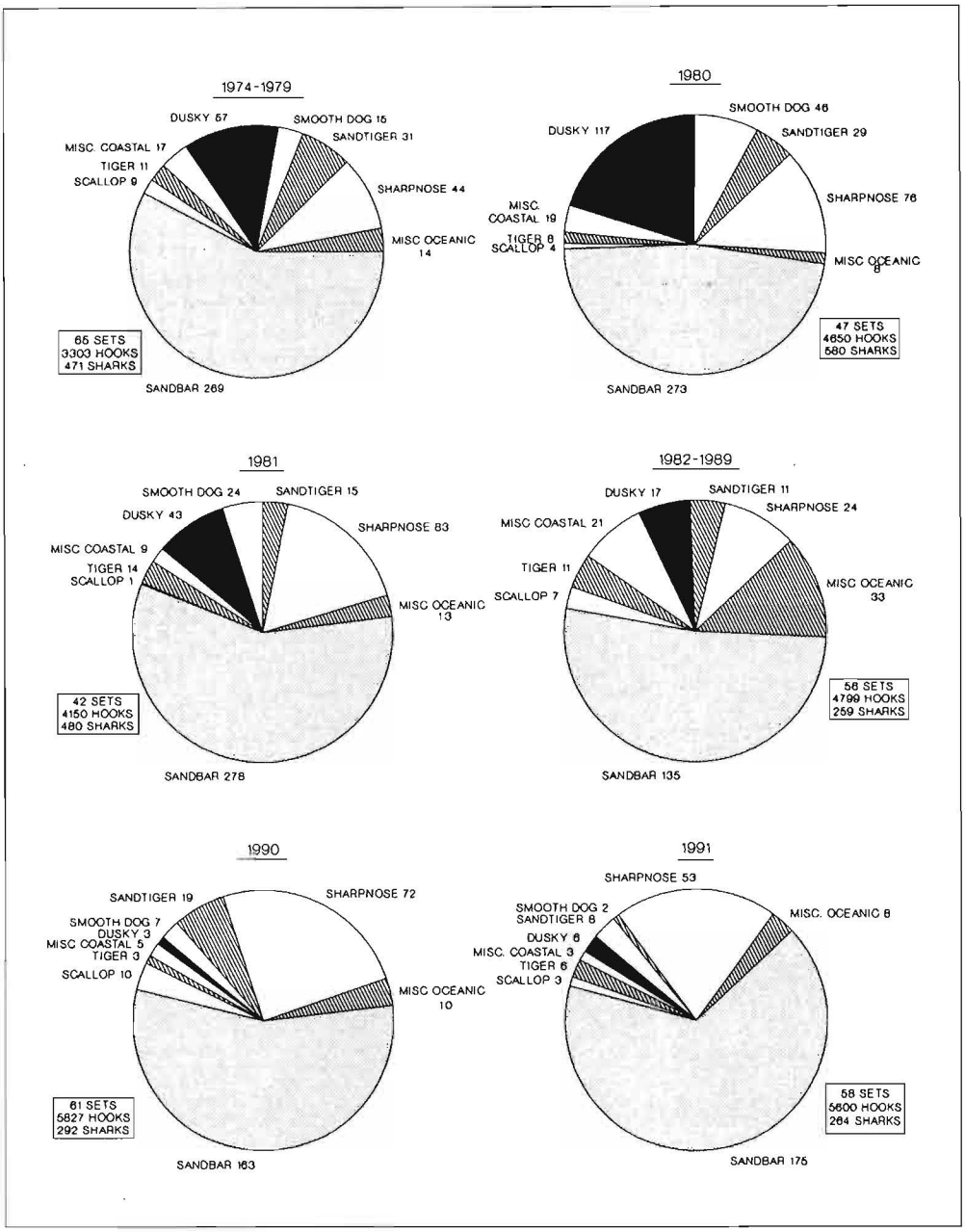

Figure 2
Relative abundance of shark species collected by VIMS longlines by year-group or year from 1974 through 1991.

the survey period (Fig. 4C). The tiger shark generally was caught at depths >10 m; catch rates in the mid-continental shelf region (10–100 m) declined almost 80% (Fig. 4E).

CPUE for two species, the Atlantic sharpnose shark (*Rhizoprionodon terraenovae*) and the scalloped hammerhead (*Sphyrna lewini*), did not show the same distinct trend in this analysis. Atlantic sharpnose sharks were taken in substantial numbers during mid-summer, but catches were sporadic and clustered, reflecting the schooling behavior of this species. Although a slight decline is suggested in Figure 4D, it is not of the magnitude shown by the other species, and normal variation in occurrence could explain this effect; however, more detailed CPUE analyses in the following sections suggested possible declines in abundance. The number of scalloped hammerheads collected was similar to that of tiger sharks, but there was not such a distinct downward trend in CPUE, although a decline is suggested by the data (Fig. 4F).

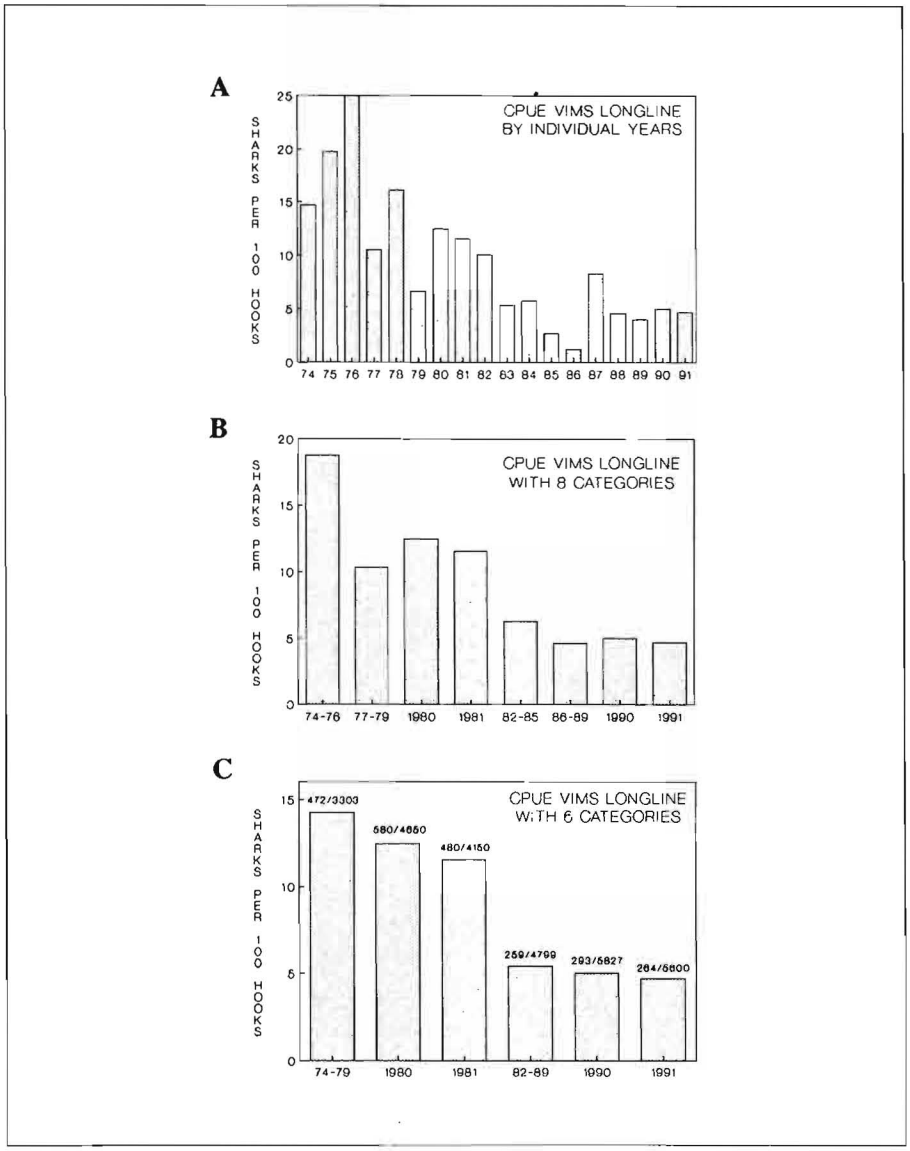

Figure 3

Three categorical analyses of catch per unit effort (CPUE) of the VIMS longline program 1974–1991. Annual catch rates (**A**) were subject to fluctuations in numbers of hooks fished, and the area and time of the effort. To offset these fluctuations, the data were categorized by varying year groups (see Table 1 for values). There was little loss of resolution between an eight category analysis (**B**) combining data over three or four year periods, and a six category analysis (**C**) which combined data for years 1974–79 and 1982–89. Thus, all analyses were performed by using the combination shown in (C). Numbers above the bars in (C) represent sharks/hooks for each category.

Catch per Unit of Effort by Depth Strata over Time

Declines in CPUE were also apparent for the various species within the various depth strata (Fig. 5). For all species combined, CPUE for each depth category (Fig. 5A) reflected the CPUE of sandbar sharks (Fig. 5B) over the same regions. Total catch rates declined in all depth categories except within Chesapeake Bay. Catches within the Bay consisted primarily of juvenile sandbar sharks.

Distinct declines across depth over time were also apparent for the dusky, sand tiger, and Atlantic sharpnose sharks (Fig. 5, C–E). The majority of dusky sharks were juveniles taken in coastal (<20 m) waters outside the Bay, although a few sub-adults and adults were taken at various continental shelf stations. Two of the three standard coastal (<10 m) stations produced

99 of the 106 juvenile (<150 cm) dusky sharks taken in that depth zone. Approximately equal numbers of dusky sharks were taken at each station, but one station was discontinued after 1983, thereby possibly biasing the apparent decline. However, CPUE for the other continuously fished coastal station also showed a similar strong decline; from 1974–81 CPUE was 43/1733 {2.48}, but from 1982–91 CPUE was 1/1486 {0.067}. The sand tiger was caught most frequently on sets made in the Bay and coastal (<10 m) waters, and CPUE declined about 75% over the survey period. (Fig. 4C) In the case of the Atlantic sharpnose shark, a distinct decline was not apparent when looking at total CPUE over time; however, in the <10 m depth range, there was a marked decline in CPUE. In the 10–20 m depth range, where the species appeared to be most common, catch rates appeared rather stable.

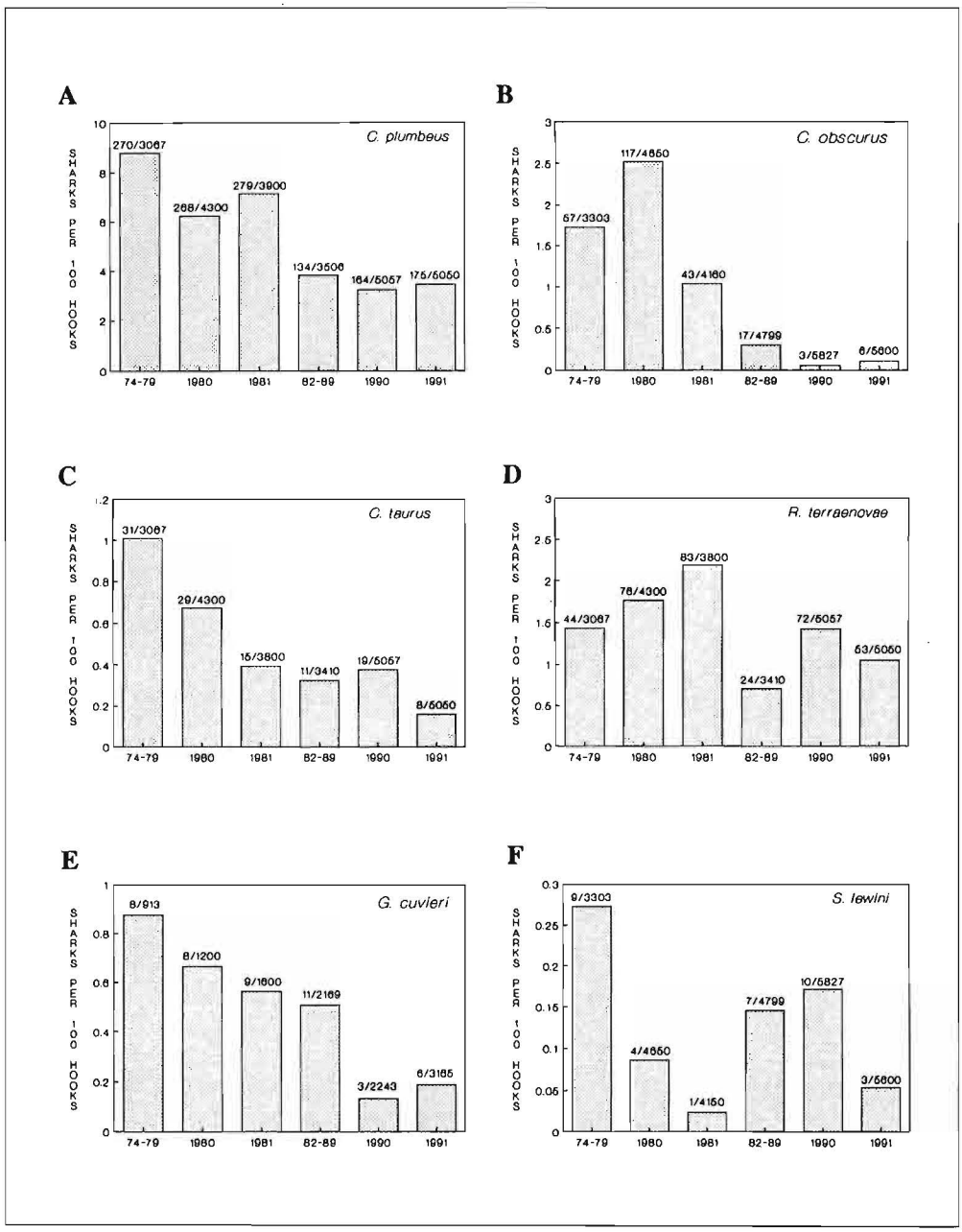

Figure 4

Catch per unit of effort for six species taken commonly on VIMS longlines, 1974–1991. (**A**) sandbar (Bay to 100 m), (**B**) dusky (Bay to >100 m), (**C**) sand tiger (Bay to 100 m), (**D**) Atlantic sharpnose (Bay to 100 m), (**E**) tiger (10-100 m), and (**F**) scalloped hammerhead sharks (Bay to >100 m). Numbers above the bars represent sharks/hooks.

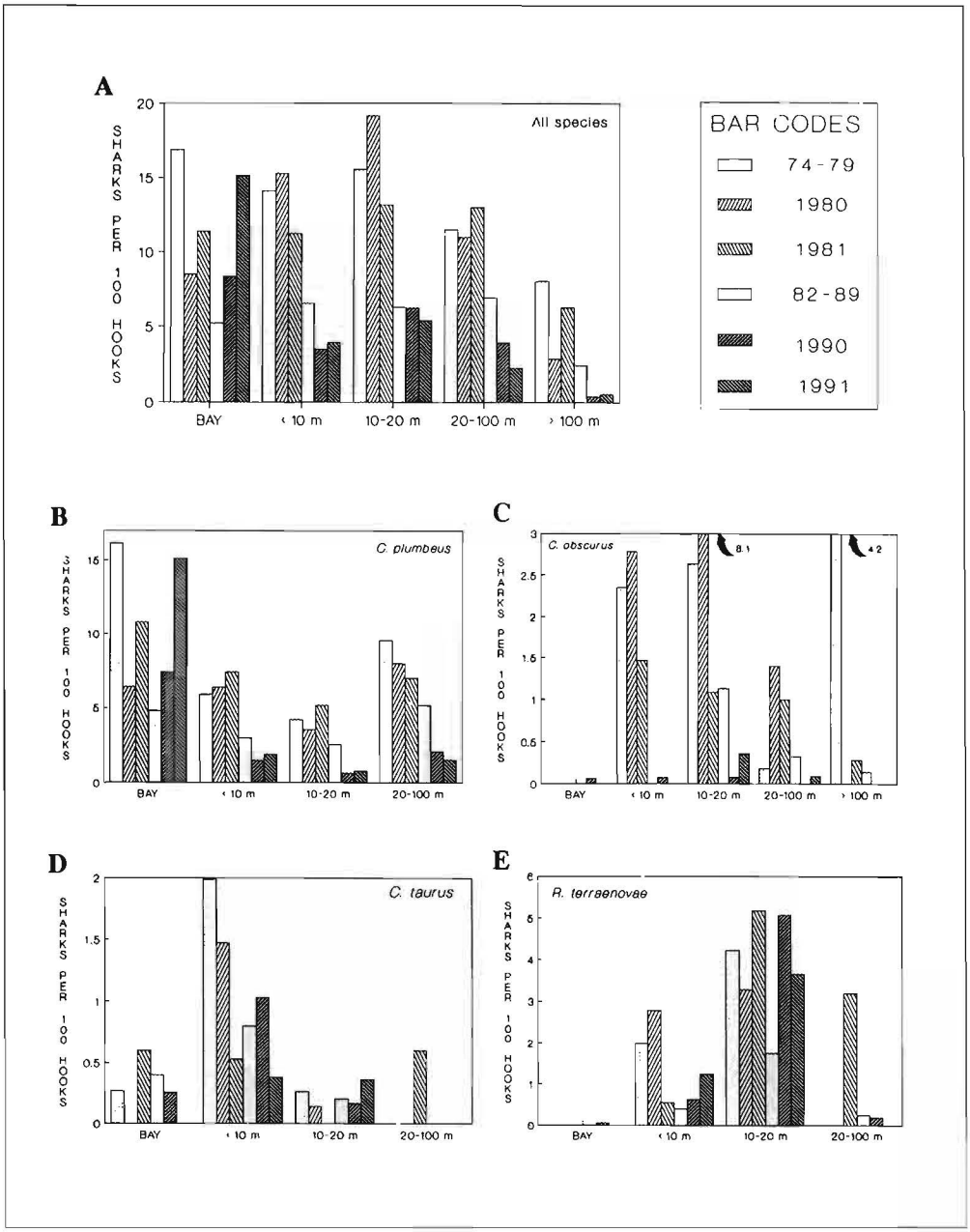

Figure 5

Shark catch per unit of effort for longlines fished in various depth strata by year category, 1974–1991. (**A**) all species combined, (**B**) sandbar, (**C**) dusky, (**D**) sand tiger, and (**E**) Atlantic sharpnose sharks.

Catch per Unit of Effort by Month over Time

Shark availability varied seasonally; thus, the declines seen over time and depth could have been affected by the months of the sampling effort in low-effort years. CPUE for all species combined showed a distinct decline by month of collection over time (Fig. 6A).

Two species — sandbar and dusky sharks — were taken in sufficient quantities over an extended period of the sampling season to permit examination of catch rates by month of capture. For the dusky shark, a graphic representation was unnecessary considering the near-total failure to capture this species in recent years. Total catch by month distinctly reflected the decline of the most common species, the sandbar shark (Fig. 6B). Sandbar sharks migrated into the Chesapeake region in May, were common throughout the summer, and began migrating south out of the area by mid-October. Catch rates have declined for all months since the early 1980's.

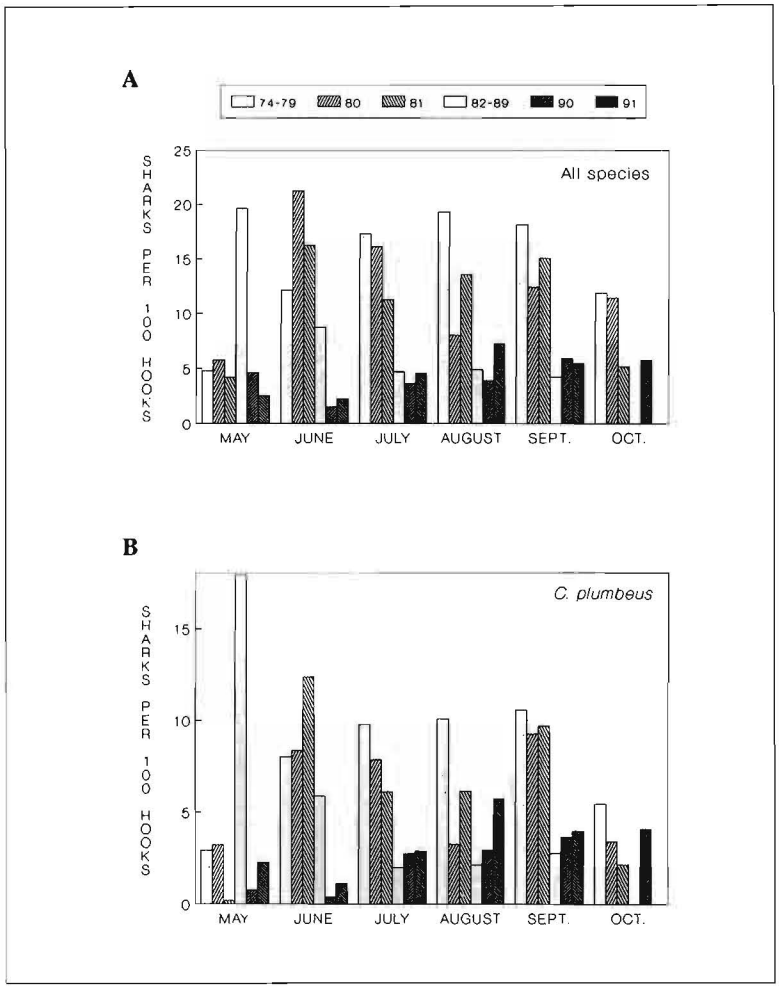

Figure 6
Shark catch per unit of effort on longlines by month by year category for (**A**) all species, and (**B**) sandbar sharks.

Catch per Unit of Effort for Size Categories of Common Species

Two species, sandbar and dusky sharks, were collected in sufficient quantities to examine CPUE by size groups. Juvenile sandbar sharks were more abundant in the lower Chesapeake Bay, whereas juvenile dusky sharks were more abundant in shallow coastal habitats outside the Bay (Musick and Colvocoresses, 1988).

The majority of sandbar sharks collected were juveniles and adolescents, 50–150 cm TL, taken in bay and coastal (<10 m) waters, whereas sub-adults and adults were more common in waters >10 m (Fig. 7A). The sandbar shark catch was categorized into four 50 cm size groups, and analyzed for CPUE by depth.

Group 1 — juveniles (50–100 cm TL)
Group 2 — adolescents (100–150 cm TL)
Group 3 — sub-adults and young adults (150–200 cm TL)
Group 4 — large adults (>200 cm TL)

These categories had some general biological significance; the majority of small sandbar sharks collected in the nursery are <100 cm TL, but adolescents use nursery grounds until they are approximately 130–150 cm TL (Casey et al., 1985; Branstetter, 1990), and the majority of sub-adults and adults taken are less than 200 cm TL (Dodrill, 1977; Branstetter, 1981b; Casey et al., 1985) (Table 4).

Catch rates differed for juvenile and adolescent fish taken in their primary habitat - Bay and coastal (<10 m) waters (Figure 7B). For juveniles 50-100 cm, CPUE declined continually until 1990. During 1990 and 1991, catch rates showed a marked increase; and reasons for this apparent increase are discussed later. In contrast, catch rates continually declined for the 100–150 cm adolescents.

Because of the overall lower number of sub-adult and adult sharks collected, data from all depths (Bay to 100 m) were used for CPUE analysis of larger fish. Again, both size groups exhibited marked declines over the survey period (Fig. 7C). This was especially true for fish

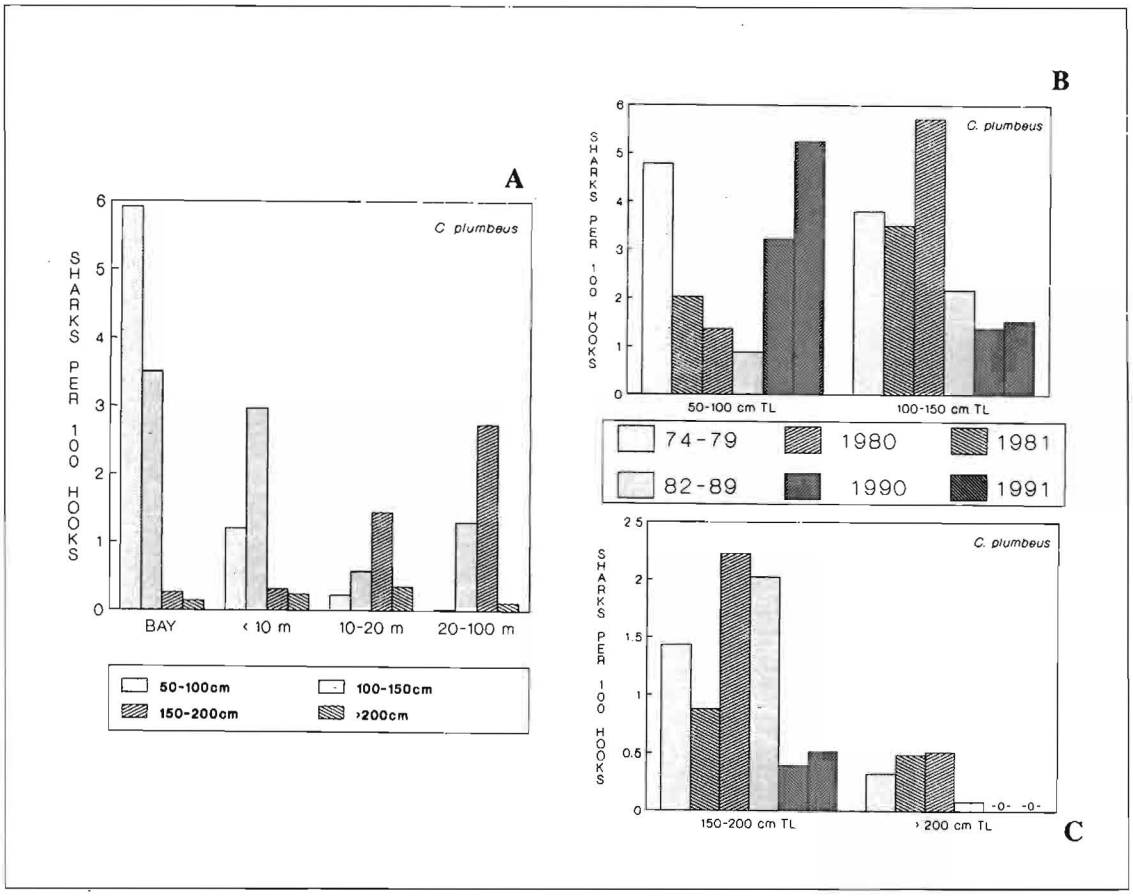

Figure 7

(**A**) Catch per unit of effort of four size classes of sandbar sharks in four depth strata illustrating the depth segregation by size class; juveniles are more common in bay and coastal waters, whereas sub-adults and adults are more common in continental shelf waters; (**B**) catch per unit of effort for two juvenile size classes of sandbar sharks taken on longlines in lower Chesapeake Bay and coastal (<10 m) waters; (**C**) catch per unit of effort for adolescent and young adults and large adults of the sandbar shark taken on longlines from the lower Chesapeake Bay to the 100-m depth contour.

>200 cm TL; since 1981, only three fish >200 cm were collected at survey sites; in 1990 and 1991, no fish were collected in this size category.

The vast majority of dusky sharks taken in the survey were juveniles (Table 5). Dusky sharks were divided into three size groups:

Group 1 — juveniles (<150 cm TL)

Group 2 — adolescents and sub-adults (150-275 cm TL)

Group 3 — adults (>275 cm).

As with the sandbar shark, these categories had a general biological significance; juveniles <150 cm TL are usually found in a nursery (Musick and Colvocoresses, 1988; Branstetter, 1990), and the species matures at approximately 275 cm TL (Compagno, 1984; Natanson, 1990). All three size classes showed a marked decline over time (Fig. 8*a*), especially juveniles. The drastic decline in CPUE of juveniles was further apparent in the CPUE analysis of this group by depth strata (Fig. 8*b*). Dusky pups rarely entered the Bay proper; only one individual has ever been taken there during the survey. Coastal (<10 m) CPUE may have been biased in that a station which produced numerous individuals was dropped from the survey after 1983. However, 1981 data for both coastal and nearshore depth categories (<10 m and 10–20 m) showed a marked decline in number of juveniles compared with the period 1974 through 1980; this reduction has continued to the present. Additionally, catches declined at stations fished continuously throughout the survey period.

Larger dusky sharks were not common in the survey (Table 5). Adolescents (150–275 cm) were taken consistently, but in low numbers each year. However, prior to a single capture in 1991, none had been taken since 1987. Mature dusky sharks (>275 cm TL) have been rare in VIMS longline collections (9 since 1974); however, the most recent captures were in 1982.

Table 4

Percent distributions of sandbar shark size classes (cm TL) collected in each depth stratum from Chesapeake Bay to the 100-m depth contour for each time-series. Some time series may not total 100% because of rounding.

	Size class (%)				Size class (%)			
Years	<100	100–150	150-200	>200	<100	100–150	150–200	>200
Bay					**<10m**			
74–79	55	38	4	3	34	50	11	5
1980	4	83	4	9	34	59	3	3
1981	17	64	10	9	17	76	7	1
82–89	33	33	22	11	11	86	4	0
1990	69	30	1	0	63	32	5	0
1991	85	15	0	0	20	60	20	0
Mean %	44	44	7	5	30	61	7	2
10–20 m					**20–100 m**			
74–79	47	47	7	0	0	33	63	4
1980	12	24	32	32	3	30	60	8
1981	0	16	67	18	0	17	81	2
82–89	4	8	84	4	0	28	70	2
1990	13	38	50	0	0	36	64	0
1991	0	44	56	0	0	50	50	0
Mean %	13	30	49	9	1	32	65	3

Discussion

The VIMS longline catch was dominated by the sandbar shark. Large sandbar sharks use the mid- Atlantic region seasonally as a feeding ground; more importantly, the bays, inlets, and barrier island areas from Chesapeake Bay to New Jersey are a major nursery ground for this species (Milstein, 1978; Medved and Marshall, 1981, 1983; Casey et al., 1985; Musick and Colvocoresses, 1988). Juveniles occupy these areas during the summer for the first several years of life until they are 130–150 cm TL, moving offshore and south in winter, and returning in the spring (Casey et al., 1985; Musick and Colvocoresses, 1988). Use of nursery grounds may reduce juvenile mortality associated with predation by larger sharks (Branstetter, 1990).

CPUE increased markedly within the Bay for 1990 and 1991 (Fig. 5A), primarily from catches of juvenile (50–100 cm TL) sandbar sharks in their nursery ground (Table 4; Fig. 7B). Although this phenomenon is similar to a documented proliferation of juvenile dusky sharks off South Africa (van der Elst, 1979) which was associated with a drastic decline in large predatory sharks. The apparent increase in relative abundance of small sandbar sharks that we observed in Chesapeake Bay may also be due to increased survivorship of young of the year, because of a large decline (60–80%) in large coastal sharks that are their principal predators. Regardless, this compensatory mechanism can be only temporary at best as the remaining mature females are captured by the fishery.

This abundance of small, juvenile sandbar sharks within Chesapeake Bay artifically inflated the overall catch rates during this time period; overall catch rates appeared to be relatively stable since the early 1980's (Fig. 3). Exclusion of all Bay efforts removed this bias and indicated a continued decline in CPUE, even between 1990 and 1991 (Fig. 9). By excluding efforts in the sandbar shark nursery ground, where individuals are concentrated in specific areas, this analysis provides a more realistic trend in shark population abundance for the region over time.

Table 5

Catch by year category of dusky shark individuals in three size classes taken on VIMS longines, 1974-1991, from Chesapeake Bay to the 100 m depth contour.

		Size class (cm TL)		
Group	Hooks	<150	150–275	>275
74–79	3067	37	4	6
1980	4300	105	12	0
1981	3800	28	12	1
82–89	3410	5	8	2
1990	5057	3	0	0
1991	5050	5	1	0
Total	24684	183	37	9

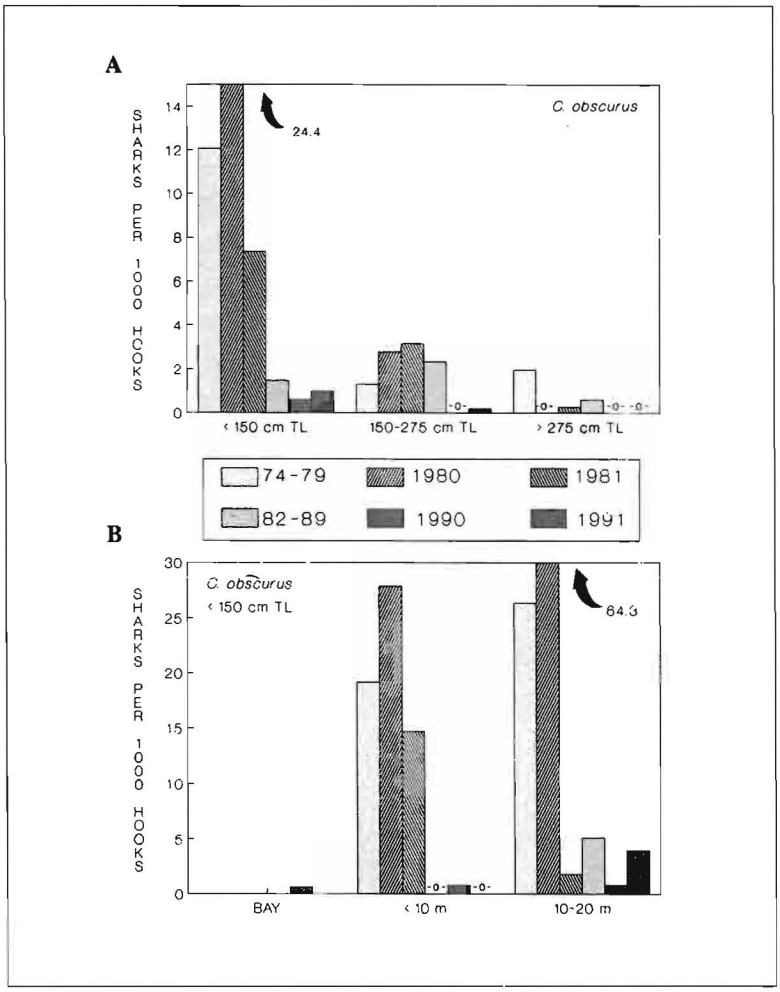

Figure 8

(**A**) Catch per unit of effort (sharks/1000 hooks) on longlines for three size classes of dusky sharks taken from Chesapeake Bay to the 100-m depth contour. (**B**) Catch per unit of effort (sharks/1000 hooks) by depth for juvenile dusky sharks (<150 cm TL) taken on longlines in lower Chesapeake Bay to the 20-m depth contour.

The biology of sharks limits their potential for exploitation (Branstetter, 1990; Pratt and Casey, 1990). This is apparently true for the sandbar shark, considering the declining CPUE's exhibited here. The species is slow-growing (K= 0.04–0.06), and does not reach maturity (>180 cm TL) until it is 13–15 years of age (Casey et al., 1985). Fecundity is low; females produce 6–10 young after a one-year gestation period, and have, at least, a one-year resting stage in the reproductive cycle. Only 25–50% of females collected are pregnant (Springer, 1960; Clark and von Schmidt, 1965; Dodrill, 1977; Cliff et al., 1989). Hypothetical maximum ages from von Bertalanffy growth models reach as high as 50 years of age (Casey et al., 1985), but this may be an artifact of the exponential nature of the model. The oldest individuals aged by analysis of vertebral ring structure have been <25 years old (Lawler, 1976; Casey et al., 1985). However, tagged juvenile sandbar sharks have been recaptured after 25 years at liberty (Casey et al., 1990, 1991); a maximum age of at least 30 years may be more realistic. Given an age at maturity of 15 years, a life span of 35 years (Hoff, 1990), and a two year reproductive cycle, each female may reproduce about ten times.

Although the biology of the dusky shark is more poorly understood, there are components of their life history that may explain the drastic decline noted here. The dusky shark is a slow-growing species (K = 0.05–0.06: Lawler, 1976; Schwartz, 1983; Natanson, 1990) that does not mature (>275 cm TL) until it is about 17 years of age (Natanson, 1990). The reproductive cycle is not well understood. Clark and von Schmidt (1965) suggested a 16-month gestation period with two dis-

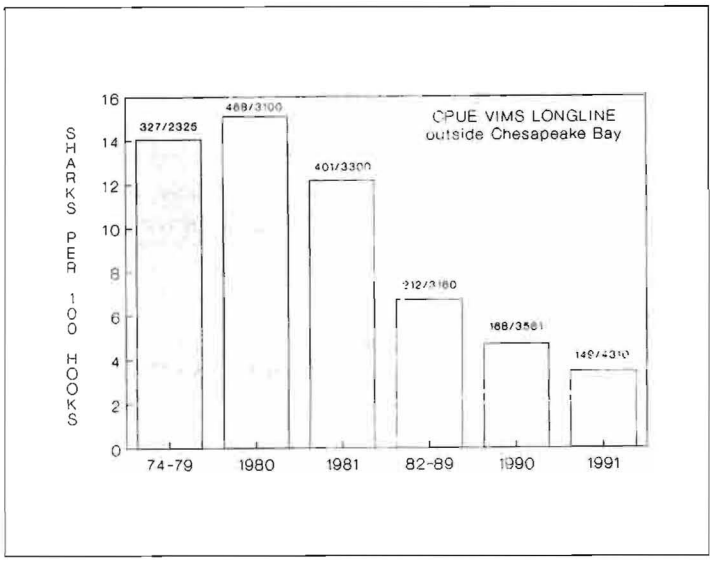

Figure 9
Catch per unit of effort on longlines fished in the Chesapeake Bight, excluding efforts in the sandbar shark nursery ground within Chesapeake Bay.

tinct reproductive groups of females: one that pupped in late June–early July, and the other in December–January. However, their data, in combination with additional literature records (Dodrill, 1977; Branstetter, 1981b), can also be used to illustrate a single-phased gestation period of about 22 months. With a one-year resting stage for post-partum females, the entire reproductive cycle would require at least three years. Dodrill (1977) noted that only about 20% of the mature females he examined were gravid. The number of young is 6–12, and most litters comprise about 10 pups (Natanson, 1990)that are correspondingly large (90–100 cm TL) in relation to the extended gestation period. The oldest specimens aged (Natanson, 1990) were 30–35 years old; thus, with a three-year reproductive cycle, the species may reproduce only about seven times.

Given the direct relationship between stock and recruitment for sharks (Holden, 1974, 1977), the declines in juvenile abundance strongly suggests a reduced parental stock size (Musick and Colvocoresses, 1988). Large dusky sharks have become a rarity in recreational fishing tournaments and commercial landings (Hueter;[1] Burgess[3]). A longer reproductive cycle, and corresponding lowered annual production, coupled with increased fishing mortality, may be important in the apparent reductions in the population size of this species over the last 10 years.

Based on their biology, estimates of the intrinsic rate of increase (r) for slow-growing species such as the sandbar and dusky sharks are between 0.015 and 0.020 (Hoenig and Gruber, 1990; Hoff, 1990). In other words, with a stable age structure, the population can increase only about 2% per year; thus there is little flexibility in the population's ability to withstand additional mortality associated with fishing (Hoff, 1990). It is probable that some of the declines of sandbar and dusky sharks are associated with the recent exponential rise in commercial efforts; both species are preferred targets of this fishery. However, the decline in the CPUE for both species in the VIMS survey began in the early 1980's, prior to the escalation of the U.S.-directed commercial fishery about 1985 (NMFS[2]). These early declines may have been associated with the combined heavy fishing pressure from 1) the recreational shark fishery that expanded rapidly along the U.S. Atlantic coast in the 1970's (Casey and Hoey, 1985), 2) the bycatch associated with an expanding swordfish and tuna longline fishery in the late 1970's and early 1980's (Berkeley and Campos, 1988), and 3) increasing foreign efforts such as the expanding Mexican shark fishery in Yucatan (Bonfil et al. 1990) that probably harvests the same stock (Hoff and Musick, 1990). Thus, the directed U.S. commercial fishery may simply have been the "straw that broke the camel's back."

In contrast to these slow-growing species, the Atlantic sharpnose shark grows rapidly, matures quickly, and reproduces often. Females mature in 3–4 years (85 cm TL), and give birth to 4–6 relatively large young (30 cm TL) after an 11–12 month gestation period (Branstetter, 1981b, 1987; Parsons, 1983 a and b, 1985). The repro-

[3]G. Burgess. Univ. Fla., Gainesville, FL, pers. commun. 1991)

ductive cycle does not include a resting stage; females mate and ovulate approximately one month after parturition (Branstetter, 1981b; Parsons, 1983b). Maximum age is estimated to be about 10 years (Branstetter, 1987). Because of its small size, this species is not targeted by commercial fishermen, however, it is a frequent bycatch on longlines targeting larger sharks (Branstetter, 1981b; Cody et al., 1981). It is also a major species taken in the recreational fishery of the southeast U.S. Atlantic coast and the Gulf of Mexico (NMFS[2]; Parrack, 1990).

The relatively rapid recruitment for this species suggests that it would be more resilient to fishing pressure than other carcharhinids. Parrack (1990) estimated that present production approximates the catch rate. However, our data indicate that CPUE may be declining for this small coastal shark. Parrack may have underestimated mortality for this species in that he did not include the significant commercial bycatch of this species in his mortality estimates; however, he did note that this species has the potential for quick recovery with a reduction of fishing effort.

Conclusions

In the recent past sharks were underutilized; 58% of the estimated recreational and commercial catch was discarded (Hoff and Musick, 1990). Apparently, however, they were not underexploited. Since 1980, the combined recreational and commercial fishing mortality has averaged 22,000 t/year (NMFS[2]); however, MSY for U.S. waters was estimated at 9,800–16,250 t (Anderson, 1985; Parrack, 1990), therefore mortality was 1.5–2.0 times MSY.

This over-exploitation is reflected in the declining CPUE for both juveniles and adults of the primary species taken in the Chesapeake Bight region of the mid-Atlantic coast. General declines in shark CPUE have been documented in both the U.S. Atlantic recreational and commercial fisheries (Parrack, 1990). Similar declines in stock abundance and size of landed fish, reflecting over-exploitation, have been noted for various shark species targeted in expanding California fisheries (Holts, 1988; Smith and Abramson, 1990), and in past elasmobranch fisheries worldwide (Aasen, 1963; Holden, 1977; Grant et al., 1979; Anderson, 1990b).

The intrinsic biological characteristics of this group of fishes makes direct exploitation of limited scope on a sustainable basis, and elasmobranch fisheries must be closely managed from the outset to avoid over- exploitation. Our data suggest that a lack of timely management contributed to a 60–80% decline in the population size of the common shark species that seasonally inhabit the mid-Atlantic region. Because these species migrate seasonally into this region from more southerly latitudes, the declines for this region are most likely representative of the stock condition throughout the majority of southeastern U.S. waters. Given the limited ability of many shark species to increase their population sizes (Hoff, 1990), this multi-species stock will take many years to recover, even after stringent management measures are implemented.

Acknowledgments

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Shark Bycatch in the Northern Gulf of Mexico Tuna Longline Fishery, 1988-91, with Observations on the Nearshore Directed Shark Fishery

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ABSTRACT

Observers aboard domestic tuna and shark longline vessels in the Gulf of Mexico from January 1988 to December 1991 recorded detailed catch and effort information from each set. A total of 87 tuna trips (302 sets) and 8 shark trips (53 sets) were surveyed, and 1,965 sharks of 18 species were recorded. The mean catch rate for the offshore tuna sets was 0.3 sharks/100 hooks, and the mean catch rate for the nearshore shark sets was 8.3 sharks/100 hooks. Shark mortality on tuna sets was 46.5% and 92.2% on shark sets. Silky sharks dominated the tuna bycatch, and substantial numbers of coastal species were caught over deep water in the vicinity of the Mississippi River Delta on tuna longlines. Dusky, thresher, and silky sharks tended to occur in deep water much farther from land (>150 km). In the combined tuna and shark set data, females predominated in the coastal species whereas males were more numerous in the pelagic species. The mean lengths of 11 species, were smaller than their reported sizes at maturity. Shark landings have declined in the Gulf since 1989 and fleet size has been reduced. A continuing observer program could be very useful to biologists conducting yearly stock assessments under the pending federal shark fishery management plan.

Introduction

Prior to the 1980's, there was little directed fishing effort for sharks in the Gulf of Mexico (hereafter referred to as the "Gulf"). Mexico's small artisanal shark fisheries in the western Gulf produced <1,000 metric tons (t) a year until 1970 when landings began to increase steadily. By 1981, Mexico's shark landings had risen to >9,000 t (Anderson, 1990) and exceeded 10,000 t/yr for the remainder of that decade. Cuba fished for sharks on the west Florida continental shelf until the late 1970's, but catches were usually less than 100 t/yr (Anderson, 1985). In 1976, Cuba's Gulf shark landings reached 1000 t, but no catches from U.S. waters have been reported since that time. A U.S. domestic shark fishery became firmly established in the northern Gulf in 1986 (NMFS[1]), although a few vessels had fished exclusively for sharks since 1981 (Miget, 1983). By 1989, there were about 55 full-time shark vessels (NMFS[1]) and 30–50 part-time shark boats in the Gulf. Shark landings peaked at over 5,600 t (Table 1), then declined sharply in 1990.

Sharks have been a substantial bycatch in other fisheries in the Gulf as well. In 1957, Japan began longlining for tuna in the Gulf (Iwamoto, 1965), and by the mid-1970's, this fishery was discarding >100 t of sharks annually (Anderson, 1985). This foreign longlining operation ceased voluntarily under an international agreement in 1982 (Honma et al., 1985). In the early 1970's, a domestic swordfish fishery became established in the Gulf (Anderson, 1990). This seasonal fishery, occurring during the fall and winter, had an estimated shark bycatch that increased from <600 t/yr in the 1970's to >1,000 t/yr in 1980 (Anderson, 1990).

Sharks were usually an unwelcome bycatch in the swordfish fishery, but this attitude changed during the mid-1980's. A domestic demand for yellowfin tuna (Adams[2]), coupled with a domestic and foreign market

[1] National Marine Fisheries Service. 1989. Draft secretarial shark fishery management plan for the Atlantic Ocean. U.S. Dep. Commer., NOAA, SE Regional Office. St. Petersburg, FL, 116 p.

[2] Adams, C. 1987. Yellowfin tuna: trends in production and value. Staff paper 308, Food and Resource Econ. Dep., Univ. Florida, Gainesville, 20 p.

Table 1
U.S. Gulf of Mexico commercial shark landings (in metric tons), 1986–91, from National Marine Fisheries Service.

Gulf state	1986	1987	1988	1989	1990	1991[a]
Florida (West Coast)	509	1,280	1,428	2,167	2,669	1,556
Alabama	213	565	314	823	653	486
Mississippi	11	74	130	60	20	54
Louisiana	72	118	2,028	2,541	772	1,105
Texas	52	22	22	26	16	16
Total	857	2,059	3,922	5,617	4,131	3,217

[a] Landings statistics for this year have not been finalized yet by NMFS.

for shark meat and fins, encouraged many swordfish longliners to target tuna and retain their shark bycatches for sale. Former shrimp trawlers, "mothballed" oilfield crew and supply boats, and newly built fishing vessels also entered this expanding fishery. The Gulf tuna longlining fleet numbered 350–400 vessels by 1988–89, and contributed greatly to Gulf shark landings after 1985 (Table 1).

Little information was available on the species composition and discard rate of the Gulf tuna fleet's shark and billfish bycatch. In October 1987, this author began a biological observer program aboard domestic tuna longline vessels in the northern Gulf. Because shark stocks were thought to be a fully or over-exploited resource by the late 1980's (NMFS[1]), observer coverage was expanded to include shark longline vessels in 1989. This paper provides a preliminary examination of shark bycatch from the tuna fleet, and observations related to the directed shark longline fishery in the northwestern Gulf.

Methods

Observers aboard domestic tuna (primarily) and shark (secondarily) longline vessels in the northern Gulf recorded information on the gear configuration and catch and bycatch composition for each set, and obtained measurements and weights (when possible) from captured fish. Vessel participation was voluntary; thus, observer coverage was not stratified by vessel type, home port, or fishing area. As the observers established contacts within the industry, a greater variety of vessels was surveyed which provided a good representation of the tuna fleet that fished from Florida to Texas. The sampled shark vessels were representative of the bottom longline fleet for shark off Louisiana. Observers did not usually make more that two consecutive trips aboard the same vessel unless the original captain and crew had been replaced after the second trip.

The observed tuna sets covered a wide area of the northern and central Gulf; most occurred shoreward of the 1829 m (1000 fm) depth contour (Fig. 1). Tuna longlines were usually set in early morning and hauled back late at night. Each set consisted of 8.1–56.4 km of mainline, 44–664 floats, and 144–1,178 8/0 circle hooks suspended by 15.2–70.4 m gangion lines. Bait was either frozen squid and herring or live chub mackerel (*Scomber japonicus*) and big-eye scad (*Selar crumenophthalmus*).

The observed shark sets were concentrated west of the Mississippi River Delta off the Louisiana coast (Fig. 1). Shark-directed sets were made at any time of the day or night and were usually hauled back after 2–8 hours of soak time. All shark sets were weighted so that the 3.0–20.9 km of mainline rested on or just above the sea floor. Gangion lines ranged from 2.7–3.7 m long and the 120–672 11/0 circle hooks were baited with dead king snake eels (*Ophichthus rex*), smooth dogfish (*Mustelus canis*), or shark pups.

Detailed effort information was recorded for each tuna or shark set along with sea surface temperatures and general biological data (species, lengths, sexes, status (live or dead) at time of capture or release) from each hooked fish. Total lengths (TL) in centimeters (cm), estimated round weight, and actual dressed weight were taken from all sharks whenever possible. For sharks cut loose alongside the boat, attempts were made to determine species and sex, and to estimate total lengths and round weights. If the observers were unsure of any shark species identification, they either photographed the fish from several angles or saved the head for later verification at the laboratory. Heads or cleaned jaws, or both, from most of the shark species encountered by the observers were archived at Louisiana State University's (LSU) Coastal Fisheries Institute.

No statistical tests were performed on the data because of yearly variations in gear configuration and geographic distribution of effort, and because of seasonal variations in observer coverage. However, catch

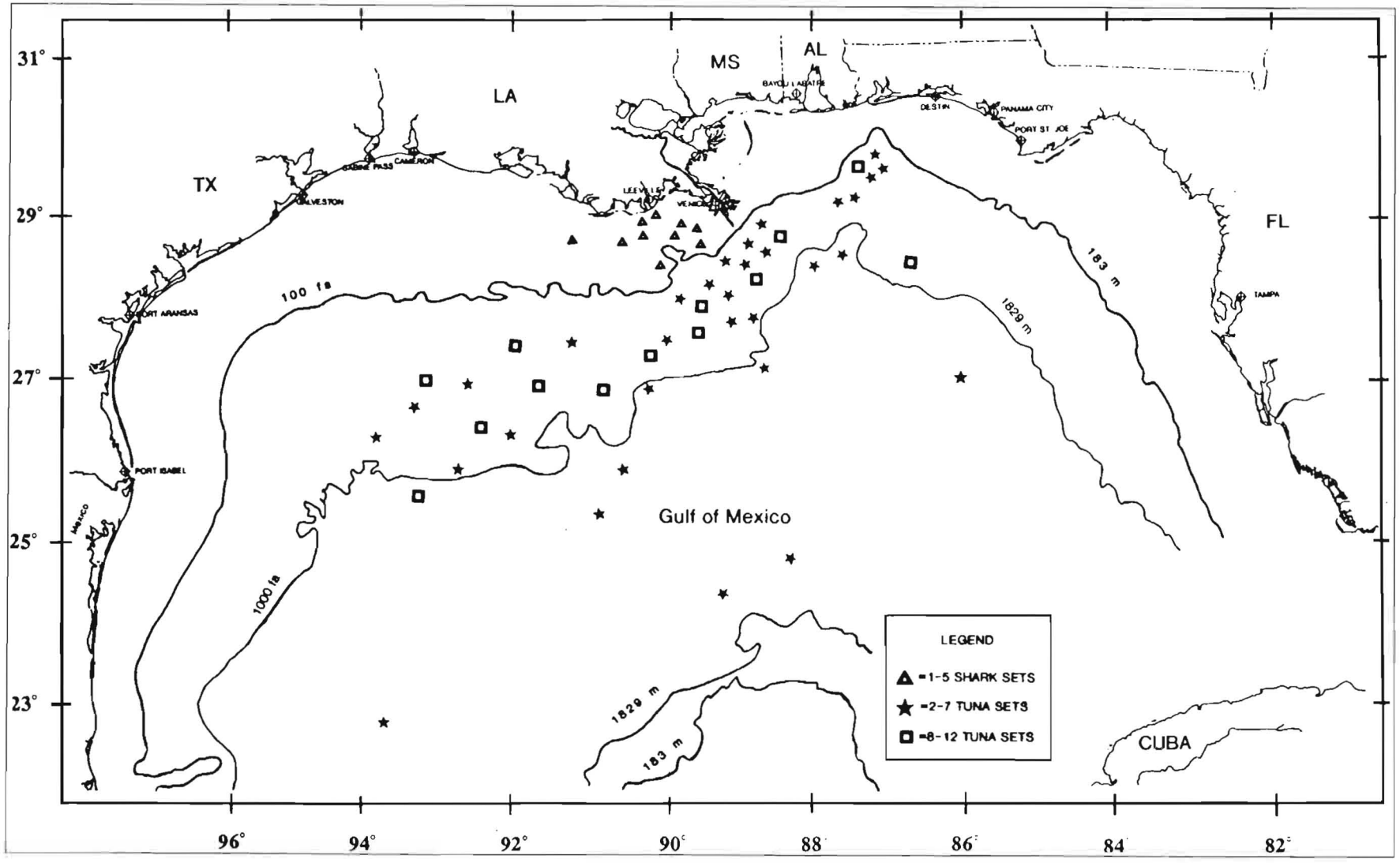

Figure 1
Locations of groups of shark sets (triangles) and tuna sets (stars and squares) surveyed by Louisiana State University observers, 1988–91.

and mortality rates, mean lengths, sex ratios, and species occurrences by depth and distance from shore were calculated and will be discussed in terms of those parameters which might be biologically significant pending further study. All common names of sharks used in this paper follow Robins et al. (1991).

Results and Discussion

Tuna Longline Bycatch

From January 1988 through December 1991, the observers recorded data from 87 trips aboard 33 different tuna vessels. The 302 sets (180,732 hooks) produced 516 sharks with an overall mean catch rate of 0.3 sharks per 100 hooks (Table 2). The mortality rate of discarded sharks was 46.5%. Causes of mortality tended to be size and species specific. Smaller individuals (<110 cm) within a species, particularly small blacktip, spinner, and silky sharks, were landed dead. Shortfin mako sharks of all sizes were apparently quite hardy; small, unmarketable individuals were usually released alive. Very large individuals within a species, particularly large bull, tiger, and sand tiger sharks, were generally quite lively when hauled up, and were released. The fate of medium to large individuals within a species was varied, although many were landed alive. Medium to large dusky, blacktip, sandbar, and silky sharks were often shot, finned, and discarded. Scalloped hammerheads were routinely shot and released (only finned occasionally) as the fishermen believed this species was responsible for most of the shark attacks on hooked tunas and swordfish. The unidentified sharks (Table 2) were those cut loose at a distance from the boats, usually at night, before the observers got a clear look at them.

The finning and shooting of sharks observed in this study were probably the reasons why the mortality rate was much higher than the rates 14.7%, 35%, and 22% reported by previous tuna longline observer studies in the Gulf (Witzell, 1985; NMFS[3, 4]); the Japanese fleet

[3] National Marine Fisheries Service. 1986. Project report: Southeast Fisheries Center domestic observer project. U.S. Dep. Commer., NOAA, Mississippi Labs., Pascagoula, unpubl. rep., 7 p.

[4] National Marine Fisheries Service. 1988. Annual report: Southeast Fisheries Center domestic longline observer project, March-December 1987. U.S. Dep. Commer., NOAA, Mississippi Labs., Pascagoula, unpubl. rep., 15 p.

Table 2
Seasonality (by month) of shark catch from tuna sets, 1988–91. J = January, F = February, M = March, etc.

Shark species	J	F	M	A	M	J	J	A	S	O	N	D	Total	No. discarded	No. discarded alive
Atlantic sharpnose												1	1	1	1
Blacktip		1	1	1		3	4	12	4	23	12		61	22	6
Bull				2	1	2		2	1				8	6	4
Dusky		1	3	3	1		1	29	1	13	2		54	48	20
Lemon										3			3	3	0
Sandbar				1	7	30	2	10		1			51	51	19
Sand tiger		1		2		5	1	9	1				18	18	13
Scalloped hammerhead		1	2	14	6	1		10		2	1		37	33	12
Unknown hammerhead										1			1	1	1
Spinner				1			12	52	1	10	2		78	67	59
Tiger		2			1		1	1	2	1			8	8	8
Unknown	1	1	1	1	1	8	7	1	3	5	6	3	38	38	37
Bigeye thresher					2			1				1	4	0	0
Longfin mako		1			1			1			1		4	2	0
Oceanic whitetip								2	2	1		1	6	5	3
Shortfin mako				2	1		1	6	2	6	2		20	6	5
Silky						5	4	35	45	10	8	2	109	82	20
Thresher		1				1	3	7		2	1		15	5	4
Total	1	9	7	26	21	55	36	178	62	78	35	8	516	396	212
No. of sets	6	24	10	13	13	21	25	66	37	34	31	22	302		
No. of hooks	3,856	11,518	5,203	5,042	8,798	11,210	12,287	39,287	26,788	21,270	20,334	15,119	180,712		

was restricted while fishing in the Gulf in 1978–81 from retaining any shark bycatch (Witzell, 1985). Finning appears to have decreased slightly in 1991 because of negative publicity which influenced many buyers to insist that carcasses be landed along with the fins. Because many tuna fishermen did not like handling shark carcasses, they discarded all sharks.

Although silky sharks were the most abundant species caught by tuna longlines in the Gulf (Table 2), only 48.3% of the 120 retained sharks were pelagic species. The next four species in order of overall abundance (spinner, blacktip, dusky, and sandbar sharks) were "coastal species" as categorized by Parrack[5]. Other tuna and swordfish gear surveys in the Gulf had also listed silky sharks as the primary species collected, but they had recorded oceanic whitetip, scalloped hammerhead, and dusky sharks as secondarily dominant (Bullis, 1976; Branstetter, 1987a; NMFS[4]).

The coastal species most often retained for sale were blacktip, spinner, and dusky sharks, and these represented 51.7% of the retained shark catch. The data from this study do not support Parrack's[5] statement that pelagic species represented 90% of the landed shark bycatch by weight in the Gulf tuna longline fishery. Parrack based his conclusion on logbook and trip ticket data, but the LSU observers noted that this data was probably suspect. They found that few tuna fishermen could accurately identify shark species, or they called everything a "mako" because mako sharks commanded the highest dockside price. Buyers seldom disputed the identification of headless, finless, and eviscerated carcasses.

Shortfin mako, thresher, bigeye thresher, large blacktip, large silky, and large spinner sharks were usually retained for sale (Table 2) if undamaged. The bigeye thresher, first recorded from the Gulf in 1980 (Branstetter and McEachran, 1983), and the thresher shark were very desirable species, contrary to Parrack's[5] finding that these species were considered unmarketable or worth so little as to be discarded at sea. Most of the bull, dusky, and sand tiger sharks were too large to be brought aboard easily and were cut loose; scalloped hammerhead, oceanic whitetip, and sandbar sharks were considered unmarketable except for their fins; all tiger and lemon sharks were cut loose immediately. Small silky and spinner sharks were generally caught in large quantities at one time; the fishermen usually finned them and discarded the carcasses.

Species composition of the shark bycatch varied by month (Table 2), and was strongly seasonal. August and October produced the most species, and January and March the least. Blacktip and dusky sharks were recorded in nine months out of the year and were most common from August through November. Sandbar sharks were recorded in six months out of the year and were most common from May through August. Scalloped hammerheads were recorded in eight months out of the year, shortfin mako and silky sharks in seven months of the year, and sand tiger, spinner, thresher, and tiger sharks in six months of the year. These variations in abundances were probably biased towards the warmer summer and fall months when longlining effort and observer coverage were apparently greatest, but they still were indicative of nearshore-offshore (or vice versa) movement patterns for some of the coastal species. For example, the shark bottom longline data showed that pregnant female blacktip sharks were abundant in nearshore waters in April and May where they probably gathered in large schools to give birth. Blacktip sharks were not caught offshore in the tuna bycatch at that time (Table 2) but appeared offshore in August after the pupping and breeding season was over.

Besides seasonal variations in species abundances, there were notable variations in species abundances by year (Table 3). Blacktip sharks were the most numerous of the shark species in the tuna bycatch in 1988, spinner sharks, followed by dusky and sandbar sharks predominated in 1989, dusky sharks predominated in 1990, and silky sharks predominated in 1991. Bull, lemon, tiger, and Atlantic sharpnose sharks were en-

Table 3
Shark catch from tuna sets by year.

Shark species	1988	1989	1990	1991
Blacktip	37	17	4	3
Spinner		76		2
Bull		6		2
Dusky		35	16	3
Sandbar		41	1	9
Sand tiger		15	2	1
Lemon	3			
Tiger	1	3	1	3
Scalloped hammerhead	2	26	3	6
Unknown hammerhead		1		
Atlantic sharpnose		1		
Shortfin mako	5	8	3	4
Longfin mako		1	1	2
Big-eye thresher		2	2	
Thresher	6	5		4
Silky		2	8	99
Oceanic whitetip		1		5
Unidentified		10	3	25
Total	54	250	44	168
No. of sets	49	85	59	109
No. of hooks	25,211	39,997	33,935	81,589
Catch rate (# fish/100 hooks)	0.2	0.6	0.1	0.2

[5] Parrack, M.L. 1990. A study of shark exploitation in U.S. Atlantic coastal waters during 1986–1989. U.S. Dep. Commer., NOAA, NMFS, SE Fisheries Science Center, Miami, FL, 14 p.

countered infrequently and apparently do not normally occur in a pelagic habitat. Other species, such as longfin mako, bigeye thresher, and oceanic whitetip sharks, are relatively rare in the Gulf, and were infrequently encountered.

The largest number of shark species was recorded by the observers in 1989 (Table 3). The highest catch rate (0.6 sharks/100 hooks) also occurred that year although the observed effort (85 sets) was not as great as the 1991 observed effort (109 sets). It appears that 1989 was an anomalous year, in both a hydrological and a biological context, because the Loop Current, an offshoot of the Gulf Stream, extended much farther northward into the Gulf for a longer period of time than normal (Schaudt et al., 1991). This giant eddy (and its associated smaller eddies) of warm water brought with it an abundance of sargassum weed, sharks, and rarely encountered species.

The small unknown hammerhead (estimated round weight=9 kg) recorded by an observer in October 1989 (it was released alive; no pictures were taken) was identified as either a scoophead (*Sphyrna media*) (Compagno, 1984) or a smalleye hammerhead (*Sphyrna tudes*) based on its distinctive head shape (as per Robins and Ray, 1986, p. 31). Neither species has been reported to occur in the Gulf (Compagno, 1984), but this shark may have moved from its more southerly habitat via the unusual Loop Current.

Likewise, in 1989, large (180–335 cm estimated total lengths) sand tiger sharks were recorded from tuna sets (Table 3) over much deeper waters (700–2450 m) than this species reportedly prefers (Compagno, 1984). No pictures were taken because most were released alive, but the observers were positive that these fish were *Carcharias taurus* as all of these sharks had equal-sized dorsal fins and darkish body spots. The sand tiger sharks may have been attracted to deeper waters by large schools of prey species brought northward by the Loop Current.

Although 1989 may have been an anomalous year in an ecological sense, catch differences in 1991 may be explained by a change in fishing techniques used by the Gulf tuna fleet. At the beginning of summer 1991, the tuna vessels switched to frozen squid for bait, rather than to live bait, and began attaching chemical light sticks to the leaders of almost every hook. Lines were set in late afternoon, rather than in early morning, soaked overnight, and hauled back early the next morning. At the same time, the gangion and float lines were shortened in order to fish the hooks 4–15 m shallower (50.4–127.4 m) than had been done in the past (Table 4). Because the lines were fished at night, sea surface temperatures at the beginning of payout (11.7°C) were also about a degree lower. The abundance of silky sharks caught by this method indicated they are apparently more nocturnal than other species.

Table 4

Range of fishing depths of the observed tuna sets by year and mean sea surface temperature at the beginning of set payout.

Year	Mean minimum fishing depth[a] (m)	Mean maximum fishing depth[b] (m)	Mean temperature (°C)
1988	54.3	142.0	12.8
1989	56.4	140.4	12.6
1990	59.0	137.4	13.4
1991	50.4	127.4	11.7

[a] Minimum fishing depth = float line length + gangion length.
[b] Maximum fishing depth = float line length + gangion length + lower point of catenary of line between floats. Catenary depth was approximated as the radius of a circle.

An examination of sea floor depths versus species occurrences over all project years (Figs. 2–4) was intriguing in that a coastal, nearshore species, the blacktip shark, occurred over a wide depth range (88–1889 m), but a more pelagic species, the thresher shark, appeared over a narrower depth range (486–1902 m). All species, however, had mean depths within the relatively narrow range of about 750–1675 m. Many of the observed tuna sets tended to be clustered shoreward of the 1829-m (1000-fm) curve in the vicinity of the Mississippi River Delta where the continental shelf drops off quite steeply relatively close to shore (Fig. 1). Distance to the nearest shoreline (of any state or country) was then determined for each shark capture to see which species were taken relatively close to shore regardless of sea floor depth.

Although many species were captured over a wide range of distances from shore, coastal species, such as blacktip and spinner sharks, had the shortest mean distances (99 km and 114 km) from shore (Fig. 3, A and B), and pelagic species, such as silky and thresher sharks (Figs. 2 and 4D), had the greatest mean distances (162 km and 241 km) from shore. Although relatively few observed tuna sets were located seaward of the 1829-m curve, more silky (Fig. 2), sandbar (Fig. 3C), and dusky sharks (Fig. 3D) were taken in the oceanic habitat beyond that contour (at least at the depths fished by the tuna gear) than others like the sand tiger (Fig. 4A), thresher (Fig. 4D), and shortfin mako (Fig. 4B) sharks.

Shark Longline Catches

From February 1989 through January 1991, the observers recorded data from eight trips aboard five different shark vessels (two full-time, three part-time). Fishing depths (analagous to sea floor depths since these were bottom longline sets) ranged from 16.5 m to 232.2 m on the continental shelf off Louisiana (Fig. 1). The 53

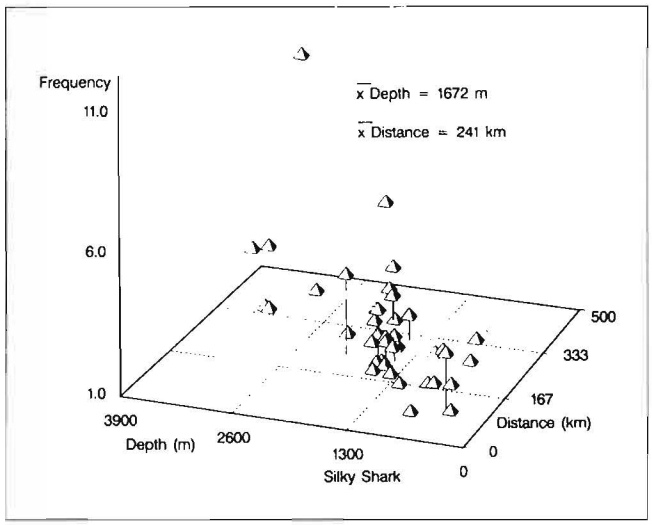

Figure 2
Numbers of silky sharks by sea floor depth and distance from nearest shoreline recorded by observers aboard tuna vessels in the Gulf of Mexico, 1988–91.

sets (17,404 hooks) produced 1,449 sharks for a mean catch rate of 8.3 sharks/100 hooks (Table 5). Overall mortality rate of the discarded sharks was 92.2%. The short gangion lines (3.1 m) restricted mobility needed for ventilation, so few sharks were landed alive.

As was expected, coastal species dominated the catches. The most abundant species overall was the blacktip shark (Table 5). Bull sharks were second in abundance of those species retained for sale. Most of the blacktip and bull sharks caught during the April and May trips were pregnant females with near full-term pups. Smooth dogfish were second in overall abundance, but these were retained for shark bait rather than for sale, as were Atlantic sharpnose sharks. Scalloped hammerheads were unmarketable and were usually finned and discarded. The only pelagic species captured (one each) were shortfin mako and silky sharks (Table 5). Dusky sharks were surprisingly rare in this nearshore fishery.

Biological Data

Owing to the nature of the commercial fisheries under observation, little biological data beyond species, total length, sex, and, occasionally, dock weight, could be gathered from each shark. The shark set data complements the tuna set data by extending areal coverage, and all biological data were combined from both fisheries. Mean lengths for females were greater than those for males except for lemon, sandbar, and oceanic whitetip sharks (Table 6). No female bigeye thresher, sand tiger, thresher, or tiger sharks were measured.

Mean lengths for male and female longfin mako, blacktip, oceanic whitetip, silky, sandbar, and spinner sharks, male shortfin mako, dusky, and thresher sharks, and female scalloped hammerhead and lemon sharks were smaller than their reported sizes at maturity (Branstetter, 1981, 1987a, 1987b; Compagno, 1984; Branstetter and McEachran, 1986; Branstetter and Stiles 1987; Berkeley and Campos, 1988; Pratt and Casey 1990). This indicates that, at least in several species, a preponderance of immature sharks were captured both in nearshore waters by the directed shark fishery, and in offshore waters by the tuna fishery. Females were more numerous than males in most of the coastal species, including blacktip, Atlantic sharpnose, bull, dusky, and spinner sharks (Table 7), but males predominated in the more pelagic species, including bigeye thresher, longfin mako, oceanic whitetip, scalloped hammerhead, shortfin mako, and silky sharks. In contrast, Berkeley and Campos (1988), who surveyed the shark bycatch in Florida's east coast commercial swordfish fishery, found that there was a preponderance of immature females in the pelagic species, and expressed concern that these sharks might be vulnerable to overfishing. However, because males and females may segregate by habitat, and because sampling was not ecologically uniform in either the aforementioned study or in this current study, these sex ratios may or may not be biologically significant in terms of stock health.

Status of the Fisheries

Since 1989, shark landings in the U.S. Gulf have steadily declined (Table 1). Tuna landings also dropped from

Table 5
Shark catch and bycatch from shark-directed sets, February 1989 to January 1991.

Shark species	No. retained	No. discarded	No. discarded alive	Total
Blacktip	666	8	0	674
Smooth dogfish	226	163	0	389
Atlantic sharpnose	167	37	0	204
Bull	43	2	2	45
Spinner	31	8	8	39
Sandbar	31	10	10	41
Lemon	8	0	—	8
Scalloped hammerhead	5	26	1	31
Dusky	2	0	—	2
Silky	1	0	—	1
Shortfin mako	1	0	—	1
Unknown	0	14	0	14
Total	1,181	268	21	1,449

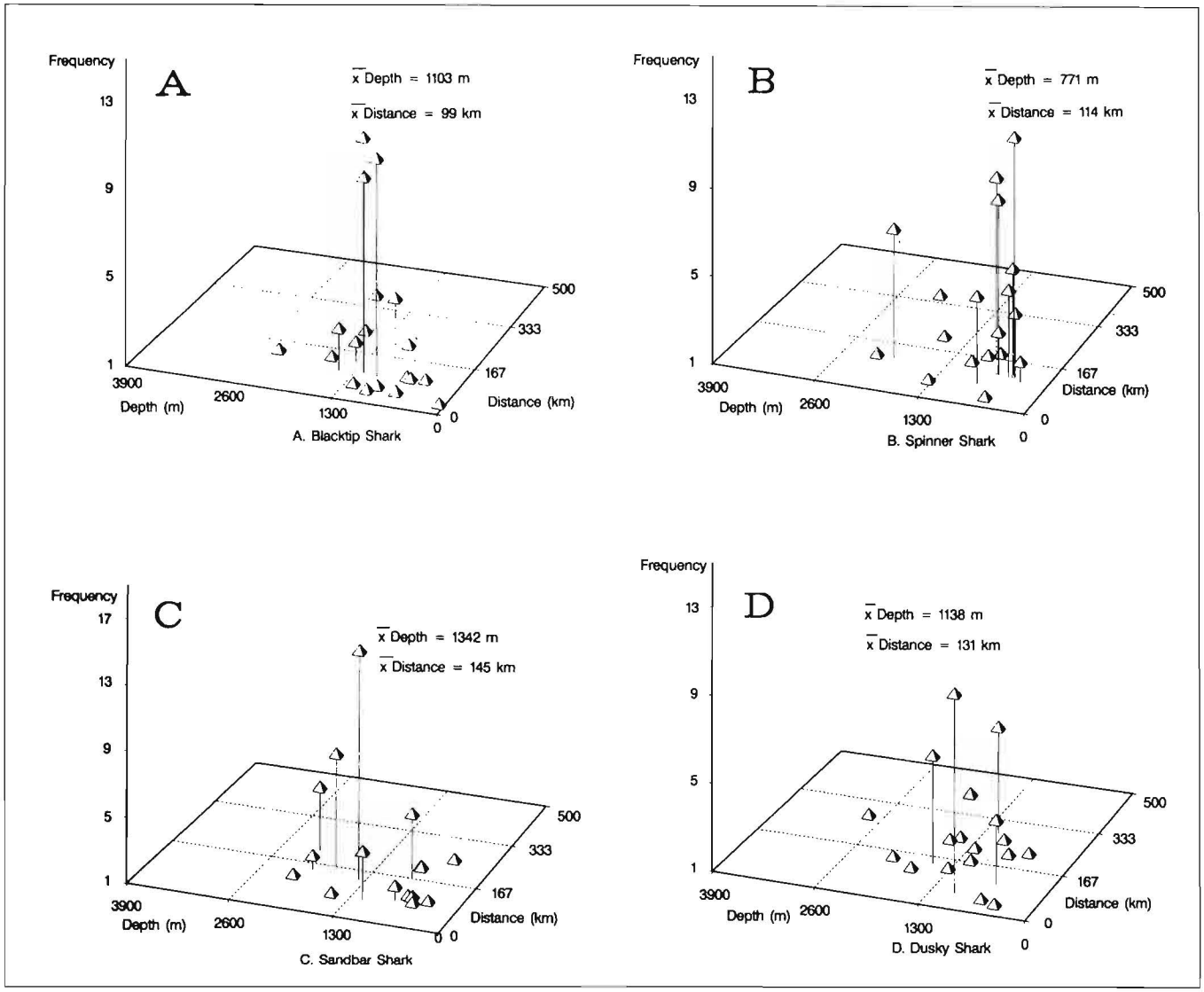

Figure 3

Numbers of blacktip sharks (**A**), spinner sharks (**B**), sandbar sharks (**C**), and dusky sharks (**D**) by sea floor depth and distance from nearest shoreline recorded by observers aboard tuna vessels in the Gulf of Mexico, 1988–91.

5,963 t in 1989 (NMFS[6]) to 3,484 t in 1991.[7] Many tuna and shark fishermen sought alternative fisheries and many vessels were either sold or returned to their original uses in the offshore oil business or the shrimp fishery. Some tuna captains took their vessels to either Guam, Hawaii, Trinidad, or Mexico in search of better fishing opportunities. Most of the very large, full-time shark vessels that had originally started fishing off Florida's west coast in the mid-1980's, and gradually worked their way westward to Louisiana, were sold and are now used in other fisheries. Based on observer and personal observations during this study, the reduced Gulf tuna and shark fleets now appear to be mainly composed of vessels with experienced, successful captains.

The huge increase in Gulf shark landings from 1986 to 1988 (Table 1), and the public outcry over the practice of finning, prompted the National Marine Fishery Service to draft a secretarial shark fishery management plan for the Atlantic Ocean (including the Gulf) to address some of these concerns over stock exploitation (NMFS[1]). Expected to become law in 1993, this plan will impose quotas on coastal and pelagic species, and will prohibit the landing of fins without the associated carcasses. Unfortunately, shark management is a complicated issue as it involves several different fisheries and species in the Gulf. Although

[6] National Marine Fisheries Service. 1990. Fishing trends and conditions in the Southeast region, 1989. U.S. Dep. Commer., NOAA, SE Fisheries Science Center, Miami, FL, 70 p.

[7] L. Usie, NMFS, New Orleans, LA; M. Hightower, NMFS, Galveston, TX; G. Davenport, NMFS, Miami, FL, all pers. commun., June 1992

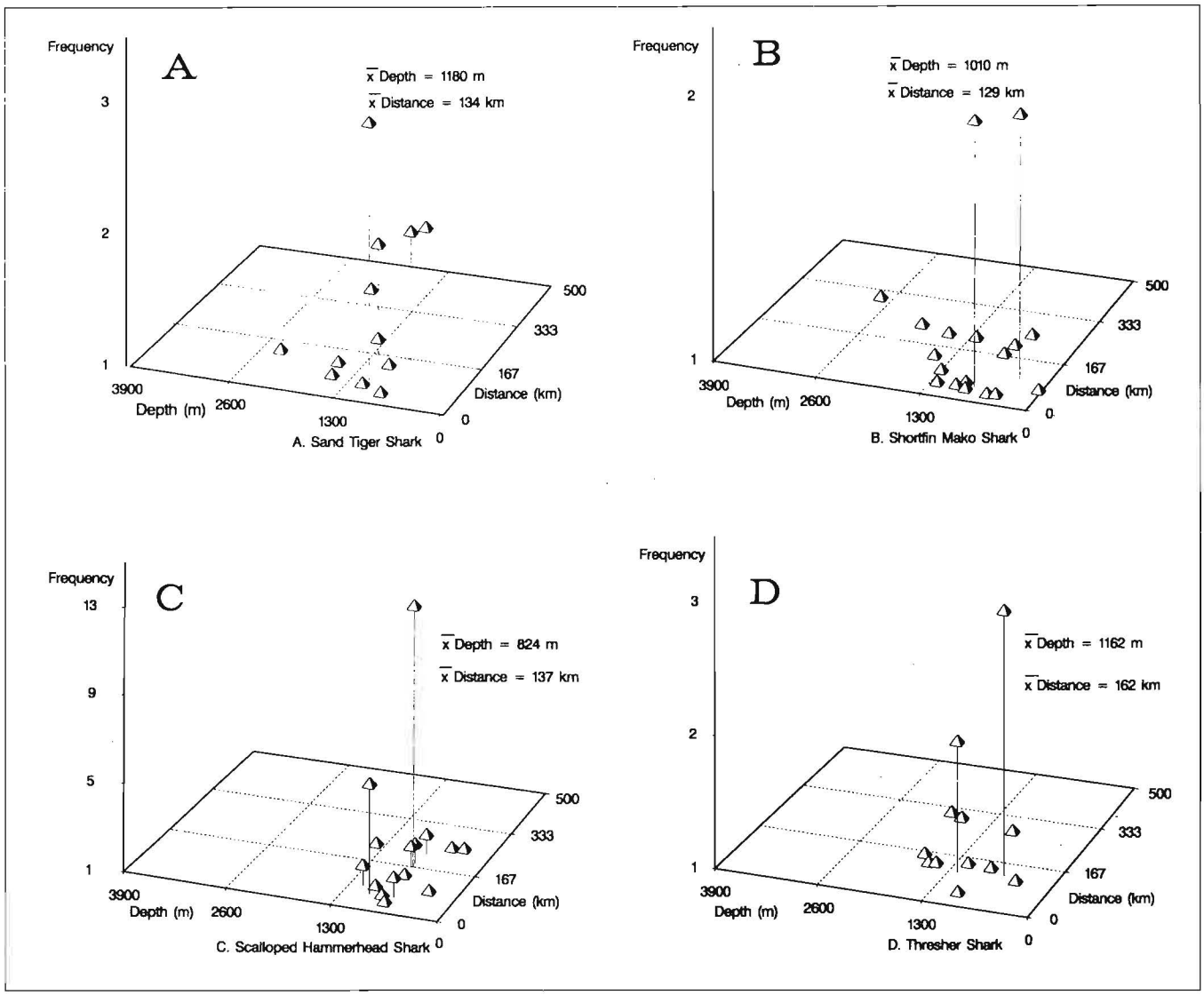

Figure 4

Numbers of sand tiger sharks (**A**), shortfin mako sharks (**B**), scalloped hammerhead sharks (**C**), and thresher sharks (**D**) by sea floor depth and distance from nearest shoreline recorded by observers aboard tuna vessels in the Gulf of Mexico, 1988–91.

quotas will effectively regulate the nearshore directed shark fishery, which catches a limited number of coastal species, quotas will do little to decrease the shark bycatch and associated mortality of the tuna and swordfish fishery. Additionally, sharks cause such damage to hooked tunas and swordfish that fishermen may continue to kill many of them unless faced with a stiff federal fine for such an offense; this measure would be nearly impossible to enforce unless observer coverage was made mandatory, greatly expanded, and tied in to the NMFS or Coast Guard enforcement network.

Under this pending shark fishery management plan, yearly stock assessments would be enhanced by the results generated from this study that showed shark landings from tuna trips were represented by more than pelagic species. Commercial shark bottom longline gear probably effectively samples many of the most common coastal shark species. These populations could be monitored via observers as this would be the only way to obtain species composition of the catches. On the other hand, tuna longline gear coverage is apparently so spotty that it would not be a reliable way of monitoring most coastal or pelagic shark populations on a yearly basis. However, placing observers aboard these vessels would complement the nearshore shark vessel effort because many highly migratory coastal species are also caught by tuna vessels. Onboard observers would be the only means of recording yearly fluctuations in species composition of the shark bycatch. Relative abundances of some of the pelagic shark species in the tuna bycatch over a period of several years might be useful indicators of the status of these populations.

Acknowledgments

Grants from the Marine Fisheries Initiative (MARFIN) Program supported this study in its entirety and were greatly appreciated. Many thanks to those captains who graciously allowed observers to go aboard their vessels, and to the dock managers and fish buyers who helped the observers establish a rapport within the industry. Invaluable technical support was received from Bruce Thompson (ichthyologist) and Glenn Garson (statistician) at LSU. Above all, the observers are to be praised for their dedication and courage in the face of often discouraging and uncomfortable circumstances.

Table 6

Mean total lengths (cm) by sex of all measured sharks caught by both tuna and shark directed sets, 1988–91.

Shark species	Male TL (*n*)	Female TL (*n*)
Atlantic sharpnose	90 (22)	94 (146)
Big-eye thresher	337 (3)	—
Blacktip	125 (156)	142 (233)
Bull	216 (6)	229 (20)
Dusky	198 (4)	284 (5)
Lemon	231 (1)	158 (6)
Longfin mako	226 (2)	241 (1)
Oceanic whitetip	167 (3)	153 (1)
Sandbar	184 (12)	158 (11)
Sand tiger	280 (1)	—
Scalloped hammerhead	202 (16)	227 (3)
Shortfin mako	188 (4)	292 (3)
Silky	87 (57)	87 (52)
Spinner	82 (40)	96 (58)
Thresher	261 (3)	—
Tiger	366 (1)	—

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Table 7

Numbers by sex of each species caught by tuna and shark directed sets, January 1988 to December 1991.

Shark Species	Tuna sets			Shark sets		
	Males	Females	Unknown	Males	Females	Unknown
Atlantic sharpnose	0	1	0	22	145	0
Big-eye thresher	3	0	1	0	0	0
Blacktip	3	5	53	155	229	132
Bull	0	2	6	6	18	4
Dusky	5	8	41	0	2	0
Lemon	0	0	3	1	6	0
Longfin mako	3	1	0	0	0	0
Oceanic whitetip	3	1	2	0	0	0
Sandbar	7	1	43	5	10	0
Sand tiger	2	0	16	0	0	0
Scalloped hammerhead	5	3	29	12	1	11
Shortfin mako	6	4	10	0	0	0
Silky	57	51	1	0	1	0
Spinner	30	41	7	10	17	1
Thresher	5	1	9	0	0	0
Tiger	1	0	7	0	0	0
Unknown species	0	1	37	0	0	0

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An Overview of Mexican Shark Fisheries, with Suggestions for Shark Conservation in Mexico

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ABSTRACT

With a known shark fauna approaching 100 species, 40 of which have direct commercial importance, Mexico has the potential for a sustained shark industry if strict conservation measures can be instituted. Shark fisheries have long been important to the Mexican economy; the oldest fishery is in Mazatlan, Sinaloa, and another is near Alvarado, Veracruz. Adequate biological and fisheries data are lacking for the two large oceanic shark faunas of Mexico. Landing data are divided into two categories: tiburones, sharks over 1.5-m total length; and cazones, less than 1.5-m total length. Thus, juveniles and adults of the same species are categorized differently which complicates fishery analyses. Management of shark resources is the responsibility of the government, and there is a vital need to sensitize the fishing secretariat concerning shark conservation.

Introduction

Sharks serve an important ecological role as apex predators, and in Mexico, they are also a strong component in marine fisheries. Shark fishing is often pursued by fishermen who lack funds for other more expensive fishing ventures. In the current fisheries that we have observed, only the meat or fins are used. When the meat cannot be refrigerated, it must be dried which requires a large amount of time and labor before it can be sold. Markets for shark meat are widespread; in the large La Viga fish market in Mexico City, sharks form an important part of the fish that are sold. Many impoverished Mexicans eat shark regularly (Applegate et. al., 1979), and several typical Mexican dishes are based on shark meat. Although present fisheries do not use skins, shark skin has long been used in Mexico and elsewhere for high quality shoes and other leather products. Additionally, there is a potential for the development of markets for other shark products.

With extensive coasts bordering both the Atlantic and Pacific Oceans, Mexico could play an important role in shark conservation. Almost half of the shark species have commercial value, and in recent year shark landings have risen dramatically (Fig. 1). Although there is an increasing interest from the Mexican government on the future of these fish, little is known about the biology or fishery aspects of this resource. The objectives of this paper are to summarize information concerning Mexican shark fisheries and comment on future needs for effective shark management.

Institutions Involved in the Shark Fishery

In Mexico there are several governmental institutions associated with the management of marine resources such as sharks. The most important of these institutions are the following:

Secretaria de Pesca (SEPESCA)

This governmental office is in charge of all legal and administrative aspects concerned with fishing in Mexico, as well as with the general management of all marine resources. Fishing permits and licenses are issued for commercial ventures and scientific research. This agency

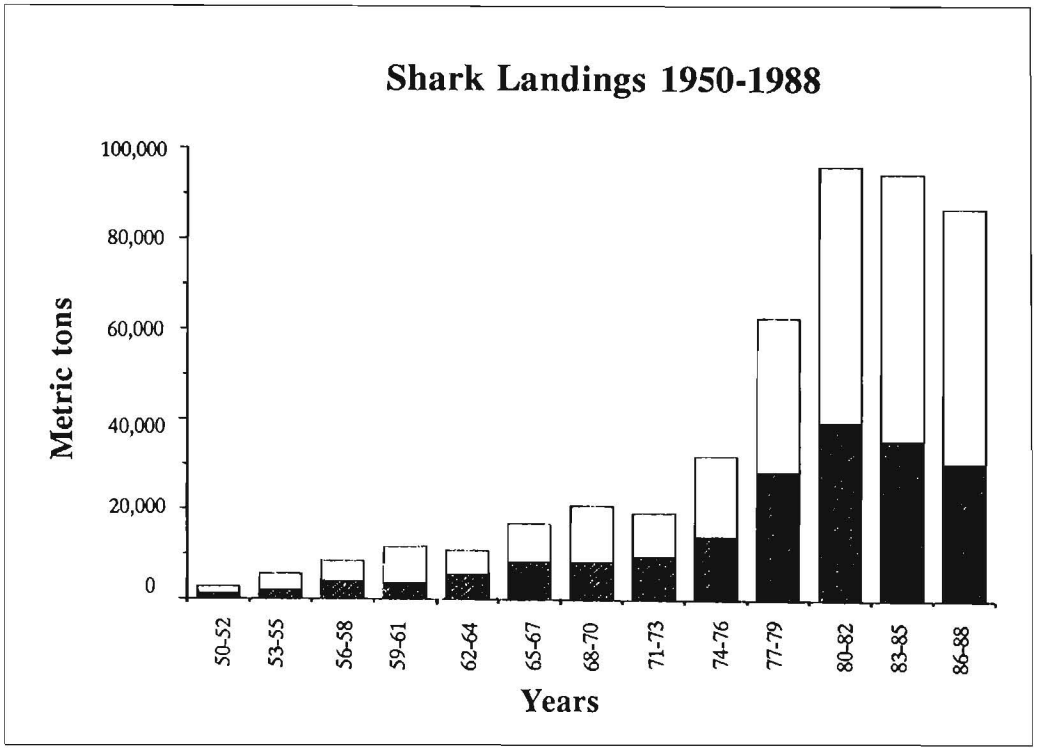

Figure 1
Shark landings (tons) in Mexico from 1950 through 1988. Darkened bar represents cazones (sharks <1 m in length); clear bar represents tiburones (sharks >1 m in length).

also keeps all the fishery statistics and formulates necessary fishing regulations.

Three fishery systems exist in Mexico and SEPESCA is responsible for managing these fishery systems. The private sector represents 60% of the fishing fleet, the cooperative sector 30%, and the other 10% is governmental. The private system uses investors to obtain fishing boats, equipment, and crew needed for fishing. Private companies pay for the licenses and permits and also pay taxes and salaries for their workers. Cooperatives exist in other areas and are usually formed by the poor fishermen, who use their limited funds in conjunction with the government to create a fishing entity, in which the fishermen jointly share the profits. Such groups are highly favored by the government.

There has been no effort to manage the fishery except for limiting the number of fishing permits. There is a growing awareness in this office for a need to conserve sharks, but activities are hindered by the lack of biological information, and the financial resources necessary to initiate a program of shark conservation. Unless these two problems are solved, shark populations may be reduced to a level where it is no longer feasible to fish for them commercially.

Directly under the Secretaria de Pesca is the Instituto Nacional de la Pesca which is dedicated to biological research and gives technical opinions on national or international research programs regarding Mexican waters. A dependency of this institution, the Centro Regional de Investigaciones Pesqueras (CRIP), carries out regional shark programs.

Secretaria de Desarrollo Urbano y Ecologia (SEDUE)

This institution is in charge of the ecological aspects and conservation of natural resources. SEDUE gives opinions on the exploitation of the Mexican fauna and flora. At present, there is no active program concerning shark conservation in this institution.

The Universidad Nacional Autonoma de Mexico(UNAM)

This is the largest university for higher education in Mexico. The Institute of Biology houses the National Fish Collections, and the Institute for Marine Sciences has a marine biological station in Mazatlan, Sinaloa and another in Puerto Morelos, Quintana Roo; both stations operate an oceanographic vessel, and both have been used for shark research. At UNAM, most of the shark investigations are carried out by the group Cipactli at the Geological Institute which has one of the largest archives concerning sharks in Mexico.

Secretaria de Educacion Publica(SEP)

SEP is in charge of all federal schools and museums, and regulates private education and technological institutes. One of its dependencies directly concerned with fishing is Unidad en Ciencia y Tecologia del Mar. Here students are trained in the field of fishing technology, engineering, and biology. This Unidad has worked in conjunction with UNAM on shark taxonomy, fishing arts, and industrial use of shark products, and has supported research leading to several scientific publications (e.g. Applegate et al., 1979).

Secretaria de Marina

This is the Mexican Navy, which is responsible for guarding Mexican waters within the 200 mile exclusive economic zone. Permits to enter and leave Mexican ports must be obtained from the Navy. The Navy has a center for biological investigation and, in the past, has shown a keen interest in shark studies. The Navy would be very important in any national plan for shark conservation.

Consejo Nacional de Ciencia y Tecnologia(CONACyT)

This is the federal funding agency for scientific research in Mexico. In the past, CONACyT supported a project carried out by the group Cipactli, from the Geological Institute, which resulted in one of the first studies to be done on Mexican Caribbean sharks (Applegate[1]).

Historical Aspects of the Fishery and Scientific Research

We believe that shark fishing is a very old Mexican endeavor; fisheries undoubtedly existed the last century. Until the Second World War, little was published concerning the Mexican shark fishery. Much of what we have discovered concerning the history of the fishery has come from personal interviews with elderly and respected fishermen, and has been incorporated in a series of unpublished technical reports available from the authors.

Pacific Coast

It is believed that shark fishing began in Mazatlan, Sinaloa. In 1870, Steindachner (*in* Beebe and Tee-Van, 1941) listed a specimen of *Triakis* taken in Mazatlan. This specimen was probably obtained from the fish market, thus an active fishery may have existed at the time. Shark fisheries were probably small, sporadic, and nomadic until the Second World War.

The lack of cod liver oil during the Second World War promoted a fishery that obtained Vitamin A and Vitamin D from the livers of sharks. This fishery was particularly strong on the Pacific coast, reaching its peak in 1944, when 9,000 metric tons were reported for the commercial catch (Castillo, 1990). Even though the synthesis of Vitamin A caused the collapse of the shark liver industry (Moss, 1989; and Castillo, 1990), this effort represents the start of the present day shark fisheries in Mexico.

According to unpublished data from SEPESCA there was a continuous increase in the captures of sharks from the early 1950's until the early 1970's. Later in this decade, the landings increased dramatically, and since the early 1980's, landings have leveled off at about 100,000 t (Fig. 1). These data apply to the country as whole, but some ports, such as Mazatlan, have shown a steady decline in catch since 1960's (Kato, 1965).

From the 1950's until present, a number of localities have been highly important to the Mexican shark fishery. Perhaps the most relevant of these fishing areas is Isla Isabela off the State of Nayarit. This island has never been continuously inhabited, but fishermen come from Teacapan and the Boca de Camichin, Nayarit, to spend one or two months a year in order to fish for sharks. This fishery appears to be healthy.

In Baja California there has been a long history of small scale shark fisheries that lasted only a short time before disappearing. In the late 1960's, a shark processing plant was developed near San Jose del Cabo, but the plant lasted less than three years. A current fishery developed in 1991, north of Santa Rosalia in Baja California Sur, targets the big-eye thresher *Alopias superciliosus*.

On the mainland, a 1970's fishery south of Isla Isabela, in Zihuatanejo, Guerrero, utilized the whole shark; perhaps for the first time in Mexico. Jaws were sold to tourists, fins were dried, the skin was taken for leather, and the oil from the livers was rendered. The remaining viscera and vertebral column were cooked, dried, and ground for use as chicken food and fertilizer. Unfortunately, the local supply of sharks was soon exhausted and boats had to go hundreds of miles to fish, thus leading to the demise of this fishery.

In the southern-most part of the Pacific region of Mexico in the late 1970's large tiger sharks, *Galeocerdo cuvier*, were fished in the states of Chiapas and Oaxaca (Avila et al., 1981). Only the meat was taken, although tiger shark skin is marketable. These fisheries do not exist today, although at the time, they appeared to show great promise.

[1] Applegate, S.P., L. Espinosa-Arrubarrena, K. Johnson-Diaz, and J.L. Cabral. 1992. Tiburones Mexicanos: area Caribena. Sec. de Pesca. Mem. del taller de trabajo y ciclo de conferencias de tiburones de Mexico y Australia (17-19 Marzo de 1992). In house publ., Instituto Nacional de la Pesca.

Atlantic Coast

Some fishing ports in the Gulf of Mexico, such as Alvarado, Veracruz, and Campeche, Campeche, may equal Mazatlan in the age of their commercial fisheries, and the development of their shark fisheries has been similar to that of the Pacific. In Tecolutla, Veracruz, in the late 1970's, numerous large boats fished as far north as Tampico. Meat and skins were sold. The catch included bull (*Carcharhinus leucas*), sandbar (*C. plumbeus*), blacktip (*C. limbatus*), dusky (*C. obscurus*), blacknose (*C. acronotus*), and Atlantic sharpnose (*Rhizoprionodon terraenovae*) sharks, plus various smoothhounds (*Mustelus spp*). In northern Yucatan, at the port of Progreso, there is a fishery that may be reaching equilibrium (Bonfil, et al., 1990). If this is so, conservation measures will be needed to sustain this important fishery.

Research Programs

In the 1960's the first cooperative project began between the Instituto de Investigaciones Biologico-Pesqueras (Instituto Nacional de la Pesca) and the U.S. Bureau of Fish and Wildlife (National Marine Fisheries Service). The objective of this six- year project was to identify the species that inhibited in the Mexican Pacific and to develop an extensive tagging program (Kato and Carvallo, 1967).

Pacific studies in the late 1960's and early 1970's were continued by the Instituto Nacional de la Pesca, under the direction of Jose Luis Castro-Aguirre who studied the taxonomy of the Pacific species until 1975. The Instituto Nacional de la Pesca at Manzanillo, Colima currently sponsors a project begun in 1987 to indentify the local pelagic shark species.

On the Atlantic coast, the Instituto Nacional de la Pesca recommenced its studies of sharks in 1981, and started a project in the state of Campeche to identify the species of the area and document the importance of the fishery. The results have not been published yet. In 1985, two more areas of investigation were opened; one in northern Yucatan and the other in the Caribbean at Isla Mujeres. These studies involved basic biology and population dynamics. At the present time there are plans to link all three projects into a broad regional program with a faunal revision, a study on the potential of the fishing fleet, population dynamics, and proposals for regulations of the resource.

Need for Studies

Even with numerous research programs there have been few publications concerning Mexican sharks. Many (Springer and Wagner 1966; Castro-Aguirre, 1967, 1981; Kato et al., 1967; Taylor 1972, Taylor and Castro-Aguirre 1972; Castro-Aguirre and Bonilla 1973; Chavez-Ramos and Castro-Aguirre, 1974; Applegate et al., 1979; Compagno 1984) are taxonomic synopses. Only recently have studies begun to address population dynamics and shark resource management. Galvan et al. (1984) pioneered a study on the seasonality, food, habits and species composition of sharks near Cerralvo Island in the southern Gulf of California. Castillo (1990) reviewed research and the fisheries of Mexico, and Bonfil et al. (1990) provided an excellent discussion of the Yucatan shark fishery, including data on each species.

Species-specific shark research is desperately needed for all of Mexico. Statistics published by the Instituto Nacional de la Pesca provide only the weight of the catch in thousands of metric tons. Sharks are not identified by species, but are categorized by size. Sharks under 1.5 m are considered cazones and those larger than this, tiburones (Castillo, 1990). This division has little, if any, value for population dynamics and conservation studies.

Mexico must document the status of its shark stocks, in regard to species, fishing areas, and population size. Such data must include the localization of nurseries, seasonal abundance, and age and growth of these sharks. We have compiled a list of 85 shark species known from Mexico's 200 mile Economic Zone (Table 1). This includes some taxa that are recorded in Mexican waters for the first time. Forty species have commercial importance and two additional species may be in need of protection; whale (*Rhincodon typus*) and the basking (*Cetorhinus maximus*) sharks. These two species are not actively fished, but are probably impacted by pollution and therefore may need some protection. Because the deep-water sharks are almost completely unknown, this list will grow as our knowledge of deep-water faunas is expanded.

Steps in Conserving Mexican Shark Resources

The first step in conserving Mexican sharks involves the study of the sharks that are fished heavily at the present time. These include the bull (*Carcharhinus leucas*), dusky (*C. obsurus*), silky (*C. falciformis*), blacknose (*C. acronotus*) blacktip (*C. limbatus*), spinner (*C. brevipinna*), tiger (*Galeocerdo cuvier*), Atlantic sharpnose (*Rhizoprionodon terraenovae*), Pacific sharpnose (*R. longurio*), scalloped hammerhead (*Sphyrna lewini*), great hammerhead (*S. mokarran*), bonnethead (*Sphyrna tiburo*), and smoothhound (*Mustelus* spp.) sharks.

Nursery areas must be located and protected for the commercial species. Some of these areas have already

Table 1

A list of shark species currently known from Mexican waters. A = Species confined to the Atlantic; P = Species confined to the Pacific; A + P = Species occurring in both the Atlantic and the Pacific; commercial species marked with an asterisk (*). Species are arranged in phylogenetic sequence, and includes some species not considered valid by Compagno (1984).

	Heptranchias perlo	A
	Hexanchus griseus	A + P
	Hexanchus vitulus	A
	Notorhynchus cepedianus	P
	Echinorhinus cookei	P
	Centrophorus acus	A
	Centrophorus granulosus	A
	Centrophorus uyato	A
	Dalatias licha	A
	Etmopterus pusillus	A
	Etmoptrus schultzi	A
	Scymnodon obscurus	A
	Somniosus pacificus	P
	Squalus acanthias	P
	Squalus asper	A
	Squalus blainvillei	A
*	*Squalus cubensis*	A
	Squalus mitsukurii	A
*	*Squatina californica*	P
*	*Squatina dumeril*	A
*	*Heterodontus francisci*	P
*	*Heterodontus mexicanus*	P
*	*Ginglymostoma cirratum*	A + P
	Rhincodon typus	A + P
	Carcharias taurus	A
	Odontaspis ferox	P
	Alopias superciliosus	A + P
	Alopias pelagicus	P
*	*Alopias vulpinus*	A + P
	Cetorhinus maximus	P
*	*Carcharodon carcharias*	A + P
*	*Isurus oxyrinchus*	A + P
	Isurus paucus	A
	Lamna ditropis	P
	Apristurus brunneus	P
	Apristurus kampae	P
	Apristurus laurussoni	A
	Apristurus parvipinnis	A
	Apristurus riveri	A
	Cephaloscyllium ventrosum	P
	Cephalurus cephalus	P
	Galeus arae	A
	Galeus piperatus	P
	Parmaturus campechiensis	A
	Parmaturus xaniurus	P
	Scyliorhinus hesperius	A
	Scyliorhinus retifer	A
*	*Mustelus californicus*	P
*	*Mustelus canis*	A
*	*Mustelus dorsalis*	P
*	*Mustelus henlei*	P
*	*Mustelus lunulatus*	P
*	*Mustelus norrisi*	A
	Galeorhinus galeus	P
*	*Triakis semifasciata*	P
	Carcharhinus albimarginatus	P
*	*Carcharhinus acronotus*	A
*	*Carcharhinus altimus*	A + P
*	*Carcharhinus brachyurus*	A + P
*	*Carcharhinus brevipinna*	A
*	*Carcharhinus falciformis*	A + P
	Carcharhinus galapagensis	P
	Carcharhinus isodon	A
*	*Carcharhinus leucus*	A + P
*	*Carcharhinus limbatus*	A + P
	Carcharhinus longimanus	A + P
*	*Carcharhinus obscurus*	A + P
*	*Carcharhinus perezi*	A
*	*Carcharhinus plumbeus*	A
*	*Carcharhinus porosus*	A + P
*	*Carcharhinus signatus*	A
*	*Galeocerdo cuvier*	A + P
*	*Nasolamna velox*	P
*	*Negaprion brevirostris*	A
*	*Negaprion fronto*	P
*	*Rhizoprionodon longurio*	P
*	*Rhizoprionodon porosus*	A
*	*Rhizoprionodon terraenovae*	A
*	*Prionace glauca*	A + P
	Sphyrna corona	P
*	*Sphyrna lewini*	A + P
	Sphyrna media	A + P
*	*Sphyrna mokarran*	A + P
*	*Sphyrna tiburo*	A + P
*	*Sphyrna zygaena*	A + P

been identified for the bull shark, *Carcharhinus leucas*, in Caribbean Mexican waters (Applegate[1]). From a commercial perspective this is probably the most important species. It is used extensively in Mexico for its meat, skin, and fins, and it has a potential market for its oil. The bull shark pups in shallow bays and estuaries favoring low salinities (Compagno, 1984). Two known nursery areas in Mexico are 1) near Teacapan in an estuary of the Rio Canas and the Rio Acaponeta, south of Mazatlan, Sinaloa (reported in this paper for the first time) and 2) in Chetumal Bay in Quintana Roo. A number of small bull sharks have been collected at the first locality and raised in the aquarium at Mazatlan, where we examined them. The second locality (Chetumal Bay), so far as we know, has been fished by only our research group. Once we have studied these nurseries and located others, it might be feasible to create nearby artificial areas for young bull sharks and raise them for future release. Fishing in these areas would be easily controlled by appropriate legislation.

Another avenue of research centers on the possibility of a sport fishing tagging program. Except for the work done by Kato and Carvallo (1967), little tagging of Mexican sharks has been undertaken. Sport fishing for sharks (as an alternative catch to billfish) occurs off Mazatlan, Sinaloa. In this instance, the most common shark that we have observed is the silky shark (*Carcharhinus falciformis*). Even though these sharks occur in great numbers, there is insufficient data to know what effect this catch has on the local population. Billfish are often tagged and released, but not sharks. A tagging program could provide important data concerning the movements of this pelagic species in the Pacific. On the east coast, short fin makos (*Isurus oxyrinchus*), are common in the springtime off Cozumel Island in the Caribbean and are often taken by American and Mexican sports fishermen. These catches also represent an excellent opportunity for starting a tagging program to collect data on the distribution and seasonality of this species.

A third goal is the recognition of special areas where sharks congregate. Klimley (1981) and Klimley and Nelson (1981) have reported on the schooling scalloped hammerheads (*Sphyrna lewini*) from the southern Gulf of California. Such large concentrations of sharks are certainly subject to fishing and these areas

should be set aside as protected underwater parks. Other areas include the caves near Isla Mujeres in the State of Quintano Roo (Clark, 1975). The "sleeping sharks" found here have been the focus of attention of scuba divers from many places. Therefore, these areas must be controlled and set aside as reserves for scientific studies and for limited touristic access.

One last area of concern is the identification and quantification of bycatch that occurs from other fisheries. Numerous immature sharks are caught by shrimp trawling on both coasts; these may be sold or discarded dead. Other sources of undocumented bycatch include foreign longline and drift-net fisheries. Almost nothing is known of the shark catch associated with these fishing efforts, although such efforts will have long- term effects on the shark populations of both the Pacific and Atlantic coasts of Mexico.

Conclusions

Shark populations in Mexico are heavily exploited. There is a definite need to monitor landings accurately by species, as well as a heed to develop a sustained tagging program and to locate the nursery areas of the Mexican commercial species. There is a need to train students in the biology of sharks and to expand governmental fishery programs that will lead to effective management regulations for sharks. In the areas where we are lacking the expertise and economic support to completely implement research programs, we must seek the aid of foreign investigators to collaborate in the study of Mexican shark faunas. For the time being, this seems the only possibility to sustain and manage this resource that is vital to the Mexican economy.

Acknowledgments

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Status and Review of the California Skate Fishery

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ABSTRACT

California commercial skate landings for 1916-90 have ranged from 22.865 metric tons (t) to 286.349 t annually. Landings from central California account for 72% of the total skate catch; the north and south regions contribute 20% and 8%, respectively. Since 1916, skate landings have represented an annual mean of 11.8% of the total California commercial elasmobranch landings. Skate landing fluctuations are correlated with changes in California trawl fisheries. There is no evidence of seasonal landing patterns (by month) but there appears to be a 20–26 year landing cycle. The biological knowledge of California's three most commercially important batoid species big skate (*Raja binoculata*), California skate (*Raja inornata*) and longnose skate (*Raja rhina*) is summarized.

Introduction

Skates are the largest and most widely distributed group of batoid fishes, with approximately 230 described species in two families (McEachran, 1990). They are benthic fishes and occur in all seas but are most common in cold temperate and polar waters. The various species range from inshore shallow waters to 3,000 m deep; however, they are limited to mid-depths along the continental shelf at tropical latitudes.

Two genera and nine species of skates in the family Rajidae occur in California waters (Eschmeyer et al., 1983; Zorzi and Anderson, 1988). Four Bathyraja species occurring in California waters are the deep sea skate (*B. abyssicola*), sandpaper skate (*B. interrupta* = *B. kincaidii*, [Ishihara and Ishiyama, 1985]), black skate (*B. trachura*) and white skate (*B. spinosissima*). Five Raja species occurring in California waters are the big skate (*R. binoculata*), California skate (*R. inornata*), longnose skate (*R. rhina*), broad skate (*R. badia*) and starry skate (*R. stellulata*). *R. badia* is a rare species with only two records from California (Zorzi and Anderson, 1988); the other four Raja species are commonly found inshore and also occur in deeper water (Eschmeyer et al., 1983). *Bathyraja* are not landed in the fishery, but three species of *Raja* are commercially used.

Natural History

Raja inornata, the California skate (Fig. 1A) ranges from the Strait of Juan De Fuca, Canada, to off central Baja California, Mexico. It is common inshore in shallow bays at depths of 18 m or less to a depth of 671 m (Eschmeyer et al., 1983). It attains a maximum total length (TL) of about 76 cm (Eschmeyer et al., 1983). Both females and males reach sexual maturity at lengths of about 52 cm (L. Martin, unpubl. data). It feeds on shrimps and probably other invertebrates. *R. inornata* is taken incidentally by trawlers and is perhaps California's most commercially important species, (Roedel and Ripley, 1950).

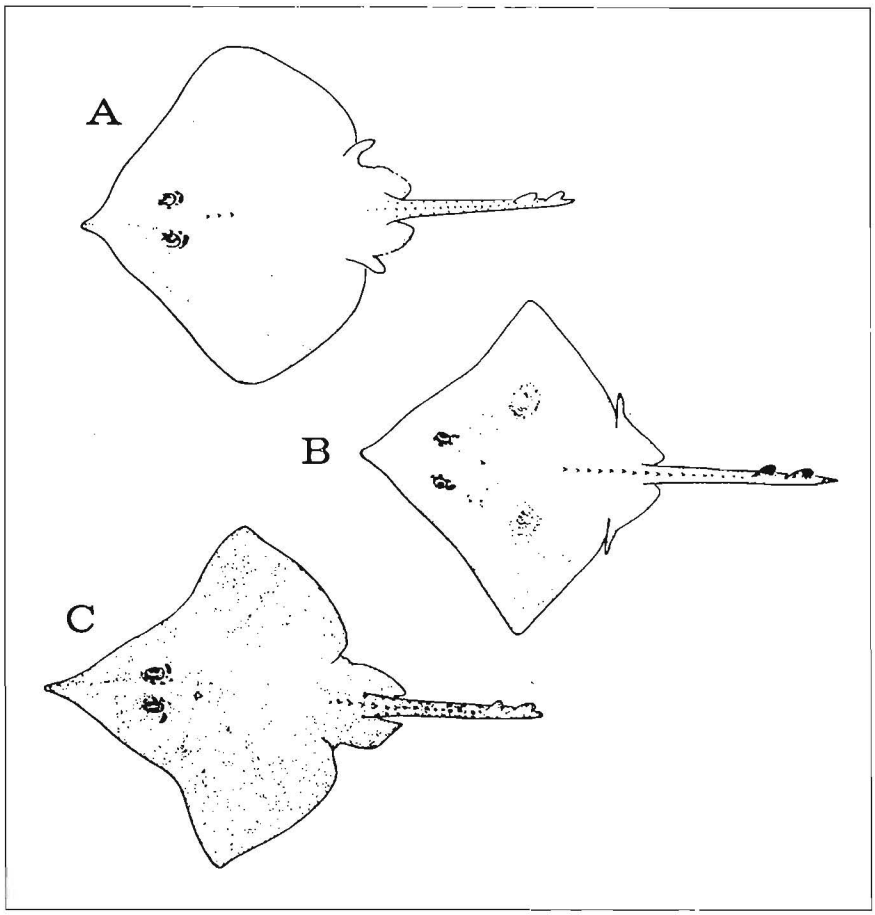

Figure 1
Three skate species occurring in the California commericial fishery: (**A**) *Raja inornata* (California skate) (**B**) *Raja binoculata* (big skate), *Raja rhina* (longnose skate). Illustrations from D.J. Miller and R.N. Lea, 1972, Guide to coastal marine fishes of California. Calif. Dep. Fish and Game Fish Bull. 157, 249 p.

Raja binoculata, the big skate (Fig. 1B), ranges from Glubokaya Bay and Cape Narvarin in the western Bering Sea to off Cedros Island, central Baja California, Mexico, but is rare south of Point Conception (Eschmeyer et al., 1983). It is found at depths of 3–800 m, but is found most frequently at moderate depths (Allen and Smith, 1988). *R. binoculata* is California's largest skate, attaining a total length of 240 cm; 180 cm and a weight of about 90.7 kg is the usual. Females mature at around 12 years of age and attain a TL of 130–140 cm; males mature at 7–8 years and attain 100–110 cm TL (Zeiner, 1991). This is the only known California skate with more than one embryo per egg case. Typically there are from one to seven embryos per egg case, three to four being the average (Eschmeyer et al., 1983). *R. binoculata* feed on crustaceans and fishes. Roedel and Ripley (1950) reported that *R. binoculata* was taken commonly by trawlers along northern California and occasionally by sport fishermen, particularly in Monterey Bay. They also noted that although it is an important commercial species, it is not landed in large numbers.

Raja rhina, the longnose skate (Fig. 1C) ranges from Navarin Canyon, in the Bering Sea, and Unalaska Island, in the Aleutian Islands, to off central Baja California, Mexico, where it is usually found on the bottom at depths of 25–684 m (Lamb and Edgel, 1986). *R. rhina* attains a maximum length of about 137 cm (Eschmeyer et al., 1983). Females mature at about 8 years of age and attain a total length of 70 cm; males mature at about 5 years and attain 60 cm total length (Zeiner, 1991). *R. rhina* is occasionally hooked by sport fishermen and is taken commercially with set lines or in trawls. Somewhat contradictory to Walford's (1935) note that *R. rhina* was one of the "most important" of the commercially landed skates and was frequently seen in the fresh fish market, Roedel and Ripley (1950) state that the meat is not as highly regarded as that of *R. binoculata* and *R. inornata* and that their pectoral fins are "occasionally" sold.

Templeman (1984) found that the thorny skate, *R. radiata*, moved 100–240 miles from tagging sites in 2–11 years. Although relatively little is known about the movements of *R. rhina*, *R. binoculata*, and *R. ornata*, it is possible that they migrate outside of California waters.

Use of Skate

Skates are exploited for food worldwide and represent as much as 42% (Taniuchi, 1990) to 55% (Compagno, 1990) of the total global elasmobranch catch annually. Landing records indicate that skates have been fished commercially in California since at least 1916. Little is known about the catch composition of the California skate fishery of the past several decades. According to Roedel and Ripley (1950), the three most commercially important skate species are *R. inornata*, *R. rhina*, and *R. binoculata*; the former two species are landed and marketed more frequently than the latter. Zeiner's (1991) work and work by the senior author (L. Martin, unpubl. data), both based on collections from the commercial fishery, support Roedel and Ripley's (1950) contention that *R. inornata* and *R. rhina* dominate the commercial fishery. Review of the landing data (Holts and Bedford[1]; Oliphant et al., 1990; Holtz[2]) shows that the three commercially landed skate species, collectively, have been among the ten most harvested elasmobranchs, in terms of biomass, in California since at least 1976.

Only the skinned pectoral fins, or "wings," of skates are marketed; the remainder is discarded. Before marketing, the wholesaler skins the wings, using a skinning machine (Fig. 2). Handling, processing, and storage characteristics have been described for Atlantic species by Wilhelm and Jobe (1988). Because skinning machines cannot accommodate skates weighing more than one kilogram (kg), only a small proportion of the skates caught are retained; larger skates are discarded at sea (Roedel and Ripley, 1950).

Currently skate wings are sold, fresh and fresh-frozen, predominantly in the oriental fish markets in southern California (Zorzi and Martin, 1992). Wings are also dried or salted and dehydrated for the oriental trade. Esteemed by the Japanese (Taniuchi, 1990), the dried skate wing is eaten with wine or processed into skate wing products, such as "kamaboko" (fish meat jelly [Ishihara, 1990]. In 1991, the demand for skate wings in the U.S. oriental market increased to such a level that they were imported from the orient into the southern California market. Skates have been processed for fish meal, but such enterprises have failed, usually for economic reasons (Roedel and Ripley, 1950). Skates have been used as substitutes for scallops (Griffith et al., 1984; Lamb and Edgel, 1986). The purpose of this paper is 1) to review and summarize California's annual skate landing data by region (north, central, and southern California), season, and value, 2) to compare skate landings to landings in associated fisheries, and 3) to discuss the concerns associated with an expansion of the California skate fishery.

Methods

To assess trends, published annual skate landing data (weights) for the years 1916–86 were taken from the California Department of Fish and Game's Fish Bulletin (Appendix 1), and other unpublished data for the years 1987–90 were made available by the California Department of Fish and Game and the University of California's Sea Grant Program. All weights were originally reported in pounds and were converted to metric tons (t) (2,205 pounds = 1 t).

Skate landing data from 1926 through 1990 were reviewed and summarized by statistical area, region (combined areas), and season. California's coastal waters are divided into six areas, as designated by the California Department of Fish and Game, for the purpose of reporting marine fisheries statistics (Oliphant et al., 1990). The areas were combined into three regions designated as "north," "central," and "south" (Fig. 3). Trends in landings were compared with the California landing data for rockfish and flatfish trawl and setnet fisheries and shark fisheries. General trends, or periodicity, in annual landings since 1916 were evaluated by identifying high catch years as "peak" years and low catch years as "minimum" years. The mean annual landing was calculated for peak and minimum years. The mean number of years between peak years and between minimum years, and from peak to minimum years was also calculated. General trends in landing cycles were noted (outliers within the trend were ignored).

The average number of skates landed annually from 1976 to 1990 was estimated based on 1) the relationships between the wing weight, total body weight, and total annual landings (dressed weight) and 2) the assumption that the average weight of a marketable skate equals approximately 1 kg (Roedel and Ripley, 1950; L. Martin, unpubl. data). Annual landing weights are wing weights (WW), which represent approximately 32% of total body weight (BW) (L. Martin, unpubl. data); thus, the landing data for year "y" when increased by 68% of its value and multiplied by 1000 kg per 1 t yields the

[1] Holts, D., and D. Bedford. 1989. Report of the assessment methods workshop for sharks. U.S. Dep. Commerce, NOAA, NMFS, Southwest Fish. Sci. Cent. (Pelagic Fisheries Resources, P.O. Box 271, La Jolla, CA 92038) Admin. Rep. LJ-89-11, 20 p.

[2] Holts, D., marine biologist, NMFS, Southwest Fisheries Science Center, Pelagic Fisheries Resources, P.O. 271, La Jolla, CA 92038, unpubl. data 1991.

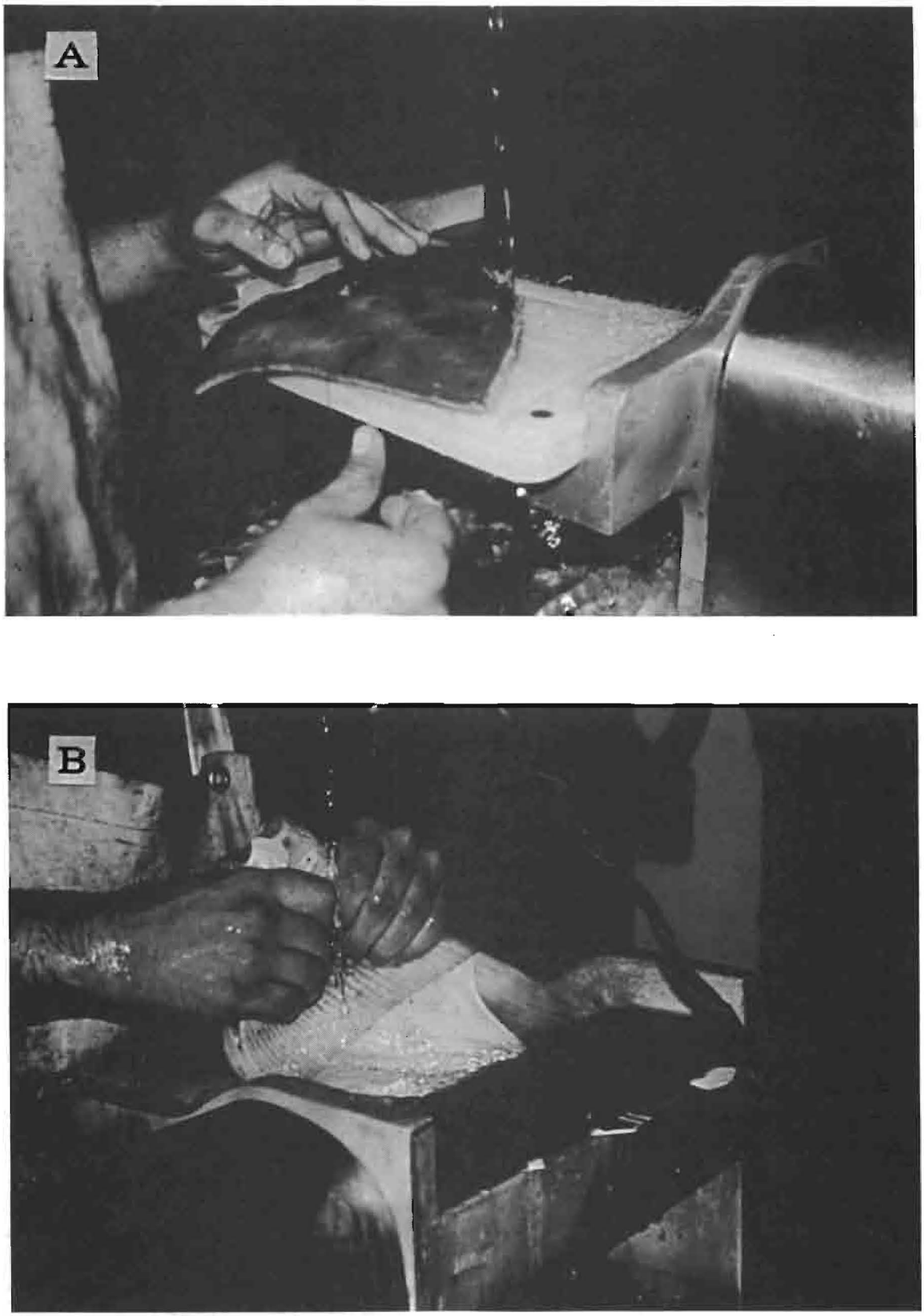

Figure 2

(**A**) Skate wing (pectoral fin), dorsal surface showing, about to be skinned. (**B**) Ventral surface of skate wing removed (dorsal surface has been skinned).

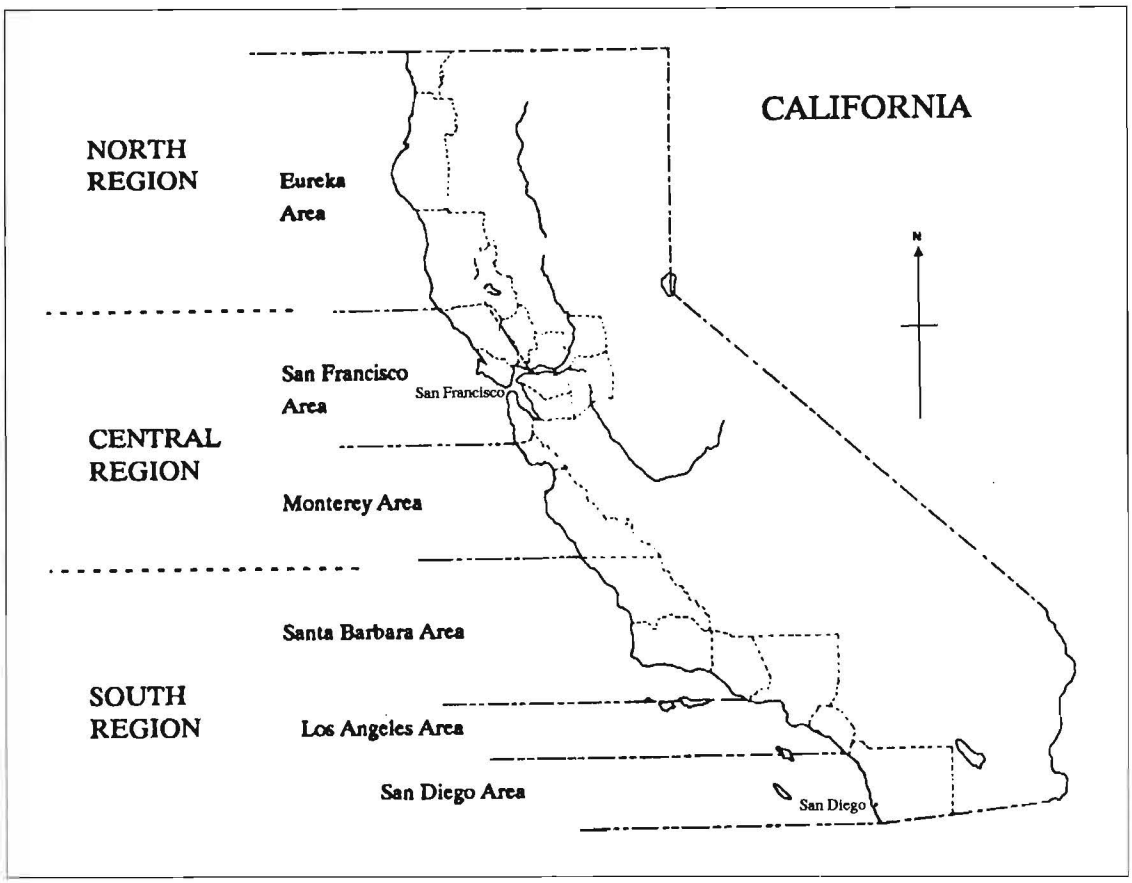

Figure 3
Map of California showing statistical areas and regions by which skate landing data were sorted.

total number of skates, with a BW of 1kg, landed that year (TSy), such that

$$[(WW_y + (WW_y \times 0.68)]t \times 1000\ kg/t = TS_y.$$

Results and Discussion

Review of the Skate Fishery

Since 1916, the annual commercial skate landings in California have ranged from 22.865 t to 286.349 t and have fluctuated widely from year to year (Fig. 4). Peak landings in 1920, 1928, 1938, 1953, 1961, and 1981 had a mean of 212.872 t (SD = 50.39 t) and ranged from 135.740 t in 1961 to 286.349 in 1981 (Table 1). Time between peaks ranged from 8 to 20 years, with a mean of 12.2 years (SD = 5.2 years). There were 14 years in which landings exceeded the lowest peak year landings (135.740 t). Minimum landings in the years 1921, 1931, 1944, 1954, 1971, and 1984 occurred from 1 to 10 years (mean = 4.5 years, SD = 3.2 yr) following each peak. The mean minimum annual landing was 46.003 t (SD = 22.234 t), ranging from 22.865 t to 79.265 t annually (Table 1). Time between minimum years ranged from 7 to 20 years, with a mean of 12.6 years (SD = 4.8 yr). There were 38 years in which landings fell below the landings in the highest minimum landing year (79.265 t).

Skate landings are probably affected by the effort and success of the target fisheries in which they occur as a bycatch. The success and effort of the target fisheries may interact such that there is little apparent correlation between landings of the target species and skate landings. For example, a high catch of the target species could result in limited storage space for skates and a subsequent drop in skate landings. According to Frey (1971) fluctuations in landings have roughly followed the trends of general economic conditions, the peaks of production occurring at about the same time as periods of economic plenty. In regard to Frey's (1971) premise, it appears that the skate landings do partially reflect changes in landings in the other California trawl fisheries, particularly in the rockfish and flatfish fisheries, but direct correlations are inconsistent and there is often a lag of several years. For example, during World War I the increased demand for protein resulted in peak rockfish landings of about 3,718.821 t in 1918, and flatfish landings peaked at about 7,709.751 t (exclusive of Pacific halibut, *Hippoglossus stenolepis*) in 1917

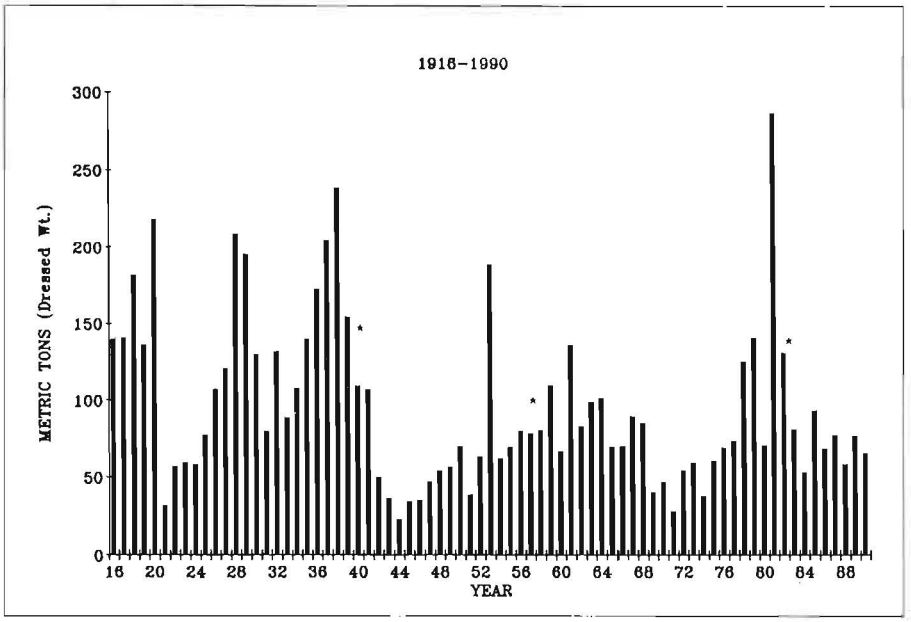

Figure 4

Annual California commercial skate landings, 1916–90. Landing data from the California Department of Fish and Game's Fish Bulletin (Appendix) and from the University of California Sea Grant Program. Asterisk (*) denotes years of El Niño events.

Table 1

California commercial elasmobranch landings in metric tons, 1916–1900. Landing data from the California Department of Fish and Game, Fish Bulletin and from the University of California Sea Grant Program.

Year	Sharks (t)	Skates (t)	Skates % total	Year	Sharks (t)	Skates (t)	Skates % total	Year	Sharks (t)	Skates (t)	Skates % total
1916	16.438	139.549	89.5	1942	1,610.63	547.930	2.9	1968	226.726	84.510	27.2
1917	130.550	142.779	52.2	1943	1,691.235	36.783	2.1	1969	156.911	40.155	20.4
1918	182.803	180.507	49.7	1944	1,185.191	22.865	1.9	1970	152.376	46.702	23.5
1919	277.852	134.145	32.6	1945	1,105.677	33.563	2.9	1971	149.655	27.769	15.7
1920	367.947	217.595	37.2	1946	729.612	35.390	4.6	1972	149.655	53.688	26.4
1921	244.588	31.714	11.5	1947	1,196.299	47.026	3.8	1973	149.655	57.616	27.8
1922	127.895	54.969	30.1	1948	1,124.932	54.012	4.6	1974	149.655	35.500	19.2
1923	163.425	60.929	27.2	1949	703.375	55.991	7.4	1975	151.469	57.433	27.5
1924	178.060	59.471	25.0	1950	325.272	69.729	17.7	1976	390.101	68.780	15.0
1925	168.853	83.210	33.0	1951	381.994	38.382	9.1	1977	627.032	73.207	10.5
1926	229.799	105.662	31.5	1952	282.638	62.908	18.2	1978	791.329	124.738	13.6
1927	147.684	119.595	44.7	1953	203.963	188.506	48.0	1979	1,042.044	140.368	11.9
1928	282.901	208.123	42.4	1954	349.348	61.776	15.0	1980	1,678.043	70.390	4.0
1929	378.212	191.649	33.6	1955	261.307	69.214	20.9	1981	1,675.481	286.349	14.6
1930	293.549	126.201	30.1	1956	492.190	79.703	13.9	1982	1,807.545	130.521	6.7
1931	270.347	79.265	22.7	1957	330.556	77.856	19.1	1983	1,429.871	84.210	5.6
1932	385.878	132.609	25.6	1958	222.992	80.222	26.5	1984	1,452.294	52.739	3.5
1933	213.612	87.846	29.1	1959	273.094	109.203	28.6	1985	1,675.514	88.812	5.0
1934	238.668	105.291	30.6	1960	314.816	66.535	17.5	1986	1,302.621	68.082	5.0
1935	251.809	137.717	35.4	1961	282.971	135.740	32.4	1987	1,180.886	69.590	5.6
1936	213.989	171.514	44.5	1962	341.566	82.618	19.5	1988	810.148	44.041	5.2
1937	414.592	202.892	32.9	1963	301.744	98.330	24.6	1989	727.385	76.420	9.5
1938	3,403.213	239.511	6.6	1964	293.219	100.997	25.6	1990	715.204	65.420	8.4
1939	4,184.785	152.704	3.5	1965	293.988	69.601	19.1				
1940	3,564.524	108.063	2.9	1966	296.494	69.845	19.1	Total			
1941	3,454.461	101.901	2.9	1967	270.693	89.227	24.8		5,3243.807	7,106.501	11.8

(Fish Bulletin no. 74; Appendix 1); this preceded the 1920 skate landings peak catch of 217.595 t (Fig. 4). The next peak in flatfish landings occurred in 1929 with over 6,349.206 t landed; between 1922 and 1926 there was also a slight increase in rockfish landings (Fish Bulletin no. 74; Appendix 1). Similarly, skate landings declined in 1921, then increased to peak in 1928 at 208.123 t. Between 1929 and 1932, during the Great Depression, flatfish landings fell to an average of 4,761.905 t annually (Fish Bulletin no 74; Appendix 1) and from 1929 through 1931 skate landings also declined. The next peak in skate landings, in 1938, may have corresponded with 1) the peak catch of flatfishes *Eopsetta jordani, Errex zachirus,* and *Platichthys stellatus* in 1939 (Frey 1971) and 2) the abrupt increase in shark landings, primarily soupfin, *Galeorhinus galeus,* caught in the bottom-fishing "set" gill net fishery in 1938. From 1939 through 1942, when many fishermen shifted to the soupfin fishery, there was a decrease in the flatfish fishery (except starry flounder, *Platichthys stellatus*) (Fish Bulletin no. 74; Appendix 1). In 1944, despite increased fishing effort, shark landings fell to about one-quarter of the record 1939 landings (Frey, 1971) and the skate fishery also reached an all time low (Fig. 4). After World War II, an expanded trawler fleet, using stronger and larger gear, fished at greater depths and in new areas, resulting in increased flatfish landings from 1945 through 1948 (Fish Bulletin nos. 74, 80; Appendix 1). The introduction of the balloon trawl net in 1943 led to a rapid expansion of the rockfish fishery, and rockfish landings increased reaching an all time high in 1958 (Fish Bulletin nos. 80, 86, 89, 95, 102, 105, 108; Appendix 1). Co-incidental with the increased effort in associated fisheries there was a steady annual increase in skate landings from 1945 to 1961, interrupted by peak landings in 1953 and concluding with the 1961 peak. This was followed by a 10-year decline to a minimum of 27.769 t in 1971. Similarly, between 1959 and 1970 rockfish landings also declined (Fish Bulletin nos. 111, 117, 121, 125, 129, 132, 135, 138, 144, 149, 153, 154; Appendix 1). The 1981 peak in skates landings was followed by a decline through 1984. Between 1984 and 1986 there was an inconsistent, but general decrease and leveling off of both rockfish and flatfish landings (Fish Bulletin no. 174; Appendix 1).

Skate Landings by Area and Region: 1948–89

Review of the skate landing data supports Frey's (1971) earlier statement that San Francisco and Monterey are the leading areas for skate landings. The central California region has dominated the state's skate catch from 1926 through 1989, accounting for 72% of cumulative total, ranging from 21–98% annually (Fig. 5,

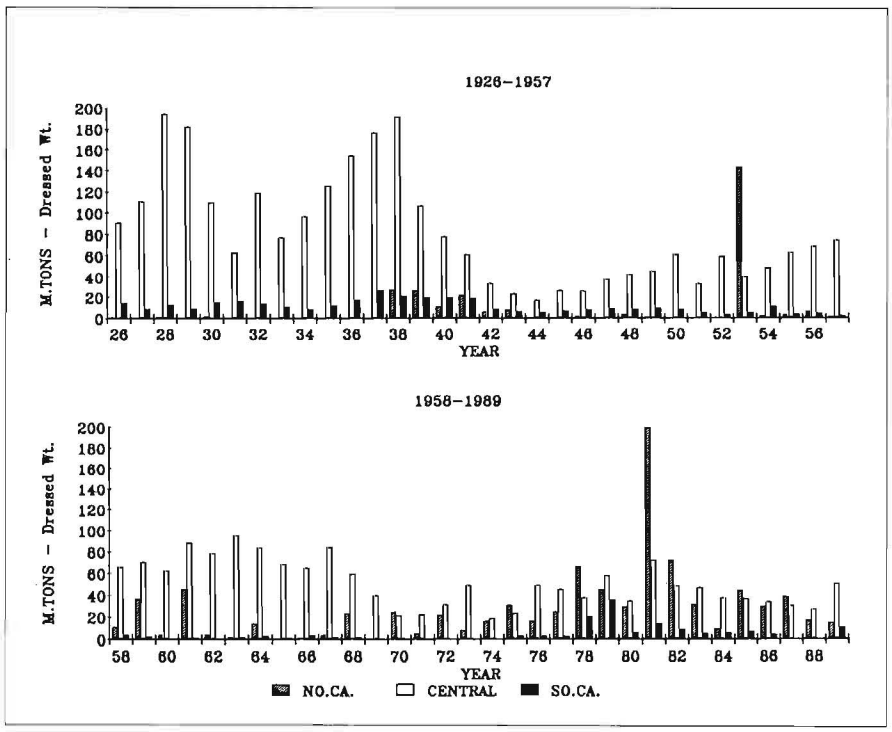

Figure 5

California commercial skate landings, by region, 1926-89. Landing data from the California Department of Fish and Game's Fish Bulletin (Appendix) and from the University of California Sea Grant Program.

Table 2

California skate landings in metric tons, by region, and as a percentage of the total state landings, 1926–1989. Landing data from the California Department of Fish and Game, Fish Bulletin, and from the University of California Sea Grant Program.

		Region					
	Total state	North		Central		Southstate	
Year	(t)	(t)	(%)	(t)	(%)	(t)	(%)
1926	105.662	0.884	0.84	90.449	85.60	14.329	13.56
1927	119.595	0.177	0.15	110.634	92.51	8.784	7.35
1928	208.123	1.061	0.51	194.128	93.28	12.933	6.21
1929	191.649	0.177	0.09	181.947	94.94	9.525	4.97
1930	126.201	1.374	1.09	109.786	86.99	15.040	11.92
1931	79.265	0.000	0.00	62.950	79.42	16.315	20.58
1932	132.609	0.000	0.00	118.616	89.45	13.993	10.55
1933	87.846	0.000	0.00	76.862	87.50	10.984	12.50
1934	105.291	0.000	0.00	96.716	91.86	8.576	8.14
1935	137.717	0.000	0.00	125.550	91.17	12.167	8.83
1936	171.514	0.000	0.00	154.354	90.00	17.160	10.00
1937	202.892	0.000	0.00	176.386	86.94	26.507	13.06
1938	239.511	27.206	11.36	191.348	79.89	20.957	8.75
1939	152.704	26.539	17.38	106.724	69.89	19.442	12.73
1940	108.063	10.770	9.97	77.852	72.04	19.441	17.99
1941	101.901	21.641	21.24	60.933	59.80	19.326	18.97
1942	47.930	6.010	12.54	33.365	69.61	8.556	17.85
1943	36.783	7.572	20.58	23.080	62.75	6.131	16.67
1944	22.865	0.295	1.29	17.060	74.61	5.510	24.10
1945	33.563	0.382	1.14	26.221	78.13	6.960	20.74
1946	35.390	1.647	4.65	25.757	72.78	7.986	22.56
1947	47.026	0.327	0.69	37.553	79.85	9.147	19.45
1948	54.012	3.265	6.05	42.241	78.21	8.506	15.75
1949	55.991	0.703	1.26	45.652	81.54	9.636	17.21
1950	69.729	0.000	0.00	61.414	88.08	8.315	11.92
1951	38.382	0.074	0.19	33.310	86.79	4.998	13.02
1952	62.908	0.209	0.33	59.598	94.74	3.101	4.93
1952	188.506	143.485	76.12	40.030	21.24	4.992	2.65
1953	61.776	1.825	2.95	48.709	78.85	11.242	18.20
1954	69.214	2.799	4.04	63.042	91.08	3.373	4.87
1955	79.703	6.351	7.97	68.732	86.24	4.620	5.80
1956	77.856	1.377	1.77	74.556	95.76	1.922	2.47
1957	80.222	10.924	13.62	65.426	81.56	3.872	4.83
1958	109.203	37.002	33.88	70.074	64.17	2.128	1.95
1960	66.635	3.788	5.68	62.391	93.63	0.456	0.68
1961	135.740	45.926	33.83	88.478	65.18	1.336	0.98
1962	82.618	3.966	4.80	78.557	94.95	0.205	0.25
1963	98.330	1.736	1.77	95.190	96.81	1.404	1.43
1964	100.997	14.027	13.89	83.987	83.16	2.983	2.95
1965	69.601	0.311	0.45	68.049	97.77	1.241	1.78
1966	69.845	1.107	1.58	65.059	93.15	3.680	5.27
1967	89.227	3.596	4.03	84.352	94.54	1.278	1.43
1968	84.510	23.451	27.75	59.957	70.52	1.462	1.73
1969	40.155	0.037	0.09	39.936	99.45	0.182	0.45
1970	46.702	24.690	52.87	21.255	45.51	0.757	1.62
1971	27.769	5.227	18.82	22.460	80.88	0.082	0.30
1972	53.688	21.769	40.55	31.467	58.61	0.452	0.84
1973	57.616	8.227	14.28	49.389	85.72	0.000	0.00
1974	35.500	16.512	46.51	18.654	52.55	0.333	0.94
1975	57.433	31.109	54.17	23.329	40.62	2.994	5.21
1976	68.780	16.789	24.41	49.193	71.52	2.798	4.07
1977	73.207	24.967	34.10	45.510	62.17	2.730	3.73

Table 2 (Continued)

Year	Total state (t)	Region					
		North		Central		Southstate	
		(t)	(%)	(t)	(%)	(t)	(%)
1978	124.738	65.966	52.88	37.881	30.37	20.891	16.75
1879	140.368	45.892	32.69	58.267	41.51	36.208	25.80
1980	70.390	29.550	41.98	34.852	49.51	5.988	8.51
1981	286.349	199.825	69.78	72.113	25.18	14.410	5.03
1982	130.521	72.365	55.44	48.913	37.47	9.243	7.08
1983	84.210	31.728	37.68	47.122	55.96	5.360	6.36
1984	52.739	37.971	17.47	37.971	72.00	5.554	10.53
1985	88.812	37.036	50.52	37.036	51.70	6.909	7.78
1986	68.082	34.209	43.72	34.209	50.25	4.104	6/03
1987	69.590	30.646	55.96	30.646	44.04	0.000	0.00
1988	44.041	26.847	39.04	26.847	60.96	0.000	0.00
1987	76.420	50.743	19.77	50.743	66.40	10.570	13.83
Total	5936.213	4274.400	19.57	4274.400	72.01	500.083	8.42

Table 2). Landings in the San Francisco area represent 71% of the central region landings and 51% of the total state landings. Landings in the Monterey area account for 29% of the central region landings and 21% of the total state landings.

Contrary to Frey's (1971) statement that few skates are landed outside of the San Francisco and Monterey areas, 28% of the skates landed since 1926 have been landed in the north and south regions combined. Twenty-percent of the total cumulative state landings were taken in the north region which had the highest landings in the years 1953, 1970, 1975, 1978, 1981, 1982, 1985, and 1987 (Fig. 5) and generally have played an increasing role since about 1970. High catches in the north region in the years 1953, 1978, and 1981 occurred in the same peak total annual catch years. Although only 8% of the total cumulative state landings were taken in the south region, this region contributed 10–24% to the total annual catch in 19 of the years between 1926 and 1954, and landings in the south region in 1926–37, 1940, 1942, 1944–52, 1954, 1955, and 1966 were greater than landings in the north (Fig. 5).

Although the skate landings in Oregon and Washington are a small percentage of their total landings, they are higher than California's annual average skate landings of 82.256 t (since 1970). In Washington alone, the average annual skate catch is 126.527 t (90.700 t from Puget Sound and 35.827 t from coastal waters) (Pattie[3]).

[3] Brad Pattie, Washington State Dep. Fisheries, 7600 Sand Point Way NE, Seattle, WA 98115. Pers. Commun. 1991.

Skate Landings by Season: 1969–89

There are no obvious trends in the skate catch related to season; however, since 1969 the greatest number of skates landed in California have tended to be taken in late winter and early spring. During this 20–year period, February and March were months of highest catch for four years. May, April, and July were highest for three, two, and two years respectively.

Skate Landing Cycles

Skate distributions and therefore landings may have been affected by fluctuations in oceanographic conditions, such as those occurring during El Niño. The effects of El Niño on the distribution of some fishes and consequent fluctuations in sport or commercial landings have been noted by several authors (Bailey and Incze, 1985; Fiedler, 1986; Mysak, 1986; Squire, 1987). Schoener and Fluharty (1985) reported three types of distributional changes in marine organisms during the El Niño years of 1940–41, 1957–58 and 1982–83 including 1) range extensions, 2) range anomalies, and 3) habitat anomalies where organisms were found shallower (deeper) or closer inshore (offshore) than normal. Karinen et al. (1985) noted the occurrence of 5 elasmobranch species outside their normal or known range during the 1981–82 El Niño. Ignoring the high catch years of 1928, 1929, and 1953, there was a periodicity to the skate landings, such that, since 1916, there have been three cycles in landings (Fig. 4). The first complete cycle began in 1921 and ended in 1944; the second cycle extended from 1944 to 1971, and the

third began in 1971 and ended around 1990. The three El Niño events of 1940–41, 1957–58, and 1982–83, which occurred 17 and 25 years apart (Fig. 4), may correlate with the 20–26 year skate landing cycle. However, because of the limited data, changes in fishing areas, and undocumented effort associated with the skate fishery, a complete assessment of the effects of El Niño on skate landings is not currently feasible.

Comparison with California Shark Landings

Annual shark and skate landings are compared in Table 1 and Figure 6. California shark landings of less than 415 t in 1937 increased to approximately 3,403.213 t in 1938, declined through the early 1950's, leveled out through the 1960's, and decreased again in the early 1970's. The rising popularity of shark in fresh fish markets in the mid-1970's accompanied an increase in the landings which peaked in the early 1980's. Since 1982 there has been a continuous decline in total west coast shark landings (Holts and Bedford[1]). Fluctuations in annual skate landings do not correlate with fluctuations in annual shark landings because 1) skates are not a bycatch of most shark fisheries and 2) the increased popularity of shark meat has not extended to skates.

FAO statistics indicate that skates may represent 42% (Taniuchi, 1990) to 55% (Compagno, 1990) of the worldwide elasmobranch catch. California's commercial skate landings have fallen both above and below these percentages, with wide fluctuations, caused by relatively large changes in total shark landings (Table 1). From 1916 to 1936, skate landings that ranged from 31.714 t in 1921 to 132.609 t in 1932 closely resembled the estimated worldwide skate-to-shark catch ratio, representing 11–89% of the total elasmobranch catch. Thirty-five percent of the 7328.205 t of elasmobranchs landed from 1916 to 1936 were skates. During the boom in shark fisheries from 1937–1948, skate landings stayed relatively constant and composed a smaller proportion of the total catch, contributing an average of 4.4% to the total elasmobranch landings. From 1949 to 1975, with a decline in shark landings, skates accounted for 20–50% of the annual elasmobranch landings and 21.1% of the total elasmobranch catch of 9518.176 t. Beginning in the mid-1970's, the rising popularity of shark as a food fish resulted in increased shark landings and hence a relative decrease in the skate proportion of the total elasmobranch catch. During 1976–90, the skate catch averaged 7.7% of the total elasmobranch catch.

Value

The economic value of the skate fishery relative to California's total commercial marine fishery is small. In the years 1957–63 and 1977–86, the skate fishery accounted for 0.003%-0.06% of the total value of fishes landed in state waters, whereas sharks accounted for 0.08%-2.4%. From 1958 to 1969 the ex-vessel price for skate wings ranged from $0.01 to $0.02 per pound and from $0.08 to $0.10 per pound for "miscellaneous" shark meat. During the 1970's the ex-vessel price for

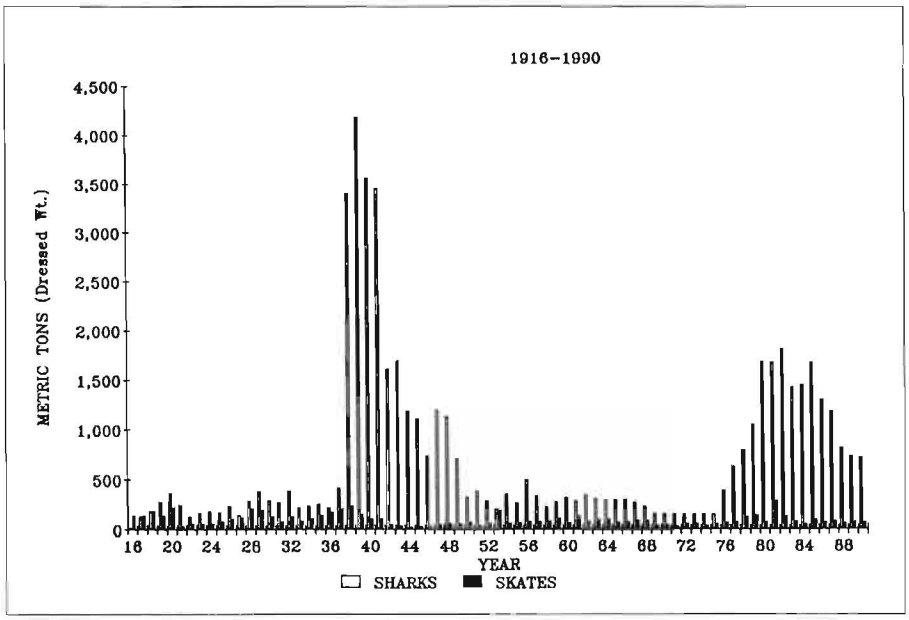

Figure 6

California commericial landings for skates and sharks, 1916–1990. Landing data from the California Department of Fish and Game's Fish Bulletin (Appendix) and from the University of California Sea Grant Program.

skates remained at about \$0.12 per pound. By 1986 the ex-vessel skate price had risen to \$0.25 per pound, but was relatively low compared with the ex-vessel price of \$0.56 per pound for miscellaneous shark and \$1.43 to \$1.60 per pound for thresher shark, *Alopias vulpinus* (Holts, 1988). The 1991 ex-vessel price for skate wings was \$0.28 per pound, whereas shark meat reached as high as \$2.40 per pound. In early 1992 skates appeared in the fresh fish market in Monterey, California, at a retail price of \$4.99 per pound, compared with \$5.50 per pound for the fairly popular shortfin mako shark (*Isurus oxyrinchus*).

The Skate Population

Based on the existing data it is not possible to determine if skate populations in California have been impacted by historic or current levels of fishing. However, there is preliminary evidence that the fishery removes high numbers of immature individuals from the skate population. The formula $[(WW^y + (WW^y \times 0.68)]t \times 1000\ kg/t = TS^y$, used to determine numbers of individual skates landed in a designated year applied to the peak year 1981 (286.349 t), yields approximately 481,000 immature skates taken from California waters and 335,700 taken from the north region alone. Approximately 154,900 skates were landed annually during the years 1976–1990 when the annual mean landing was 92.224 t. This latter figure (154,900) is a more representative estimate of the annual number of skates taken from California waters than the figure for 1981. A BW of 1 kg corresponds to a total length for *R. binoculata* and *R. rhina* of about 50 cm (Zeiner, 1991; L. Martin, unpubl. data) and ages of about 3–4 years (Zeiner, 1991) for both species. Thus, most animals landed in the fishery are well under size and age at maturity for both sexes of *R. binoculata* and *R. rhina*.

Skate Fishery Management

Like data for other elasmobranch fisheries (Hoff and Musick, 1990), landing data for skates does not accurately reflect the total biomass removed from the population, because only a small proportion of the skates caught are retained and reported in the landings (Roedel and Ripley, 1950). Although some skate species are more fecund and have higher growth rates than many shark species, compared with the bony fishes, they have relatively slow growth rates, late age at maturity, and they bear relatively few young (Holden, 1973, 1974, 1977; Ryland and Ajayi, 1984; Waring, 1984; Martin and Cailliet, 1988; Zeiner, 1991). These characteristics make all elasmobranchs vulnerable to overfishing (Holden, 1977; Compagno, 1990; Hoff and Musick, 1990; Pratt and Casey, 1990). Skates appear to have been overfished in several other areas, as indicated by the decrease in annual batoid landings over the last five years in the Japanese fishery (Taniuchi, 1990) and the diminished landings of *R. batis* in the Irish Sea fishery (Brander, 1981).

The appearance of skate wings in the fresh fish market, selling for nearly \$5.00/lb. indicates an increase in the popularity of this food fish and a possible consequential expansion of the California skate fishery. The suggestion by Roedel and Ripley (1950) that skates represented an "under-utilized" resource may be true. Certainly skates, caught as a bycatch of another fishery and discarded because they are not economically marketable, are a wasted resource and therefore are "under-utilized." Whether or not skates are also under- or over-exploited is another question and one that this paper does not attempt to answer. However, regardless of the level of utilization and given the typical elasmobranch reproductive profile (as discussed above), if large numbers of immature individuals continue to be removed from the population, then a significant expansion of the fishery (increased exploitation) without appropriate management would be ill advised.

The information needed to produce an effective skate fishery management plan includes 1) landing data on size and sex for each species landed, 2) survival rates of skates released from the catch, 3) validation of Zeiner's (1991) age and growth work on *R. binoculata* and *R. rhina*, 4) determination of life-history parameters (growth rates, ages at maturity, age-specific fecundities, etc.) for each of the three commercial skate species and 5) determination of population characteristics, including population movements, for each species.

Finally, with skate fisheries operating in California, Oregon, and Washington, and given the absence of information on "stock" structure, it would be advisable to develop a management plan that encompasses the entire eastern Pacific region. When better data on "management units," as defined by Hoff and Musick (1990) become available, the management approach could, and should, be modified.

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Application of Mitochondrial DNA Sequence Analysis to the Problem of Species Identification of Sharks

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ABSTRACT

Efforts are currently being implemented to protect and manage specific species of sharks. This requires that species designations are accurately assigned. Unfortunately, species identification can be difficult because many species are morphologically similar and commercial fishermen often remove the fins, entrails,and heads at sea, a practice that eliminates most or all diagnostic characters used for species identification. There are a number of genetic methods that can be employed as forensic tools for identifying species from carcasses. This paper briefly reviews methods of mitochondrial DNA (mtDNA) analysis and presents some preliminary data that illustrates the potential utility of mtDNA analysis to identify species of sharks from tissue samples.

Introduction

Fisheries catch statistics reveal two important features related to sharks. First, fishing pressure on sharks is increasing (see papers in Pratt et al., 1990). Second, catch statistics are rarely compiled for individual species or even genera of sharks (FAO, 1990). Although catch statistics are kept for species of teleosts, the catch of all requiem sharks, for instance, is listed under the family designation Carcharhinidae (FAO, 1990). The Carcharhinidae encompasses a diverse assemblage of sharks with marked differences in morphology, ecology, and life history among genera and species (Compagno, 1988). The genus *Carcharhinus* itself is represented by 32 recognized species (Garrick, 1982, 1985). The breadth of biological diversity encompassed by this genus is exemplified by species such as the large and widely-distributed bull shark (*C. leucas*) that can invade freshwater habitats, the oceanic whitetip shark (*C. longimanus*) that patrols the warm epipelagic surface waters of the world's oceans, and the smalltail shark (*C. porosus*) that rarely exceeds a meter in length and is found nearshore only in the tropical eastern Pacific and western Atlantic.

Many carcharhinid sharks are phenotypically similar and are often confused taxonomically,which may explain why the species are lumped together in fisheries statistics. For example, *Carcharhinus brevipinna* and *C. limbatus* both have black-tipped fins, are morphologically similar, and the scarcity of *C. brevipinna* records may be an artifact of misidentification of this species as *C. limbatus* (Branstetter, 1982).

The problem of species identification is further compounded by the fact that once caught, sharks are frequently gutted to keep the flesh from spoiling, and the heads and fins are removed. Thus, sharks on the docks resemble torpedoes, lacking teeth and fins that serve as the best and sometimes the only diagnostic characters for identifying species (Compagno, 1984). If species of sharks are to be managed as separate gene pools, we need a method for identifying species from tissue samples that can be taken from the carcasses.

Several methods are available to identify species based on analysis of proteins and DNA. For proteins, isoelectric focusing (IEF), sodium dodecyl sulfate polyacrylamide gel electrophoresis (SDS-PAGE), and allozyme electrophoresis are efficient and rapid methods that allow identification of species from muscle tissue samples, even when tissues have been cooked (i.e. IEF [Nu el al. 1989]) or stored for long periods of time at -20°C[1]. IEF is being used by the Texas Parks and Wildlife Department and the National Marine Fisheries Ser-

[1] D. Buth, Professor, UCLA, pers. commun. 1991.

vice (Charleston, South Carolina laboratory) to identify sharks from muscle samples. Allozymes have been extensively surveyed in carcharhinid sharks (Naylor, 1989; Lavery and Shaklee, 1991; Lavery, 1992) and allelic variants have been identified that can be used to distinguish species. For example, Lavery and Shaklee (1991) identified a cryptic species of shark (*C. tilstoni*) from the phenotypically similar blacktip shark (*C. limbatus*) on the basis of a few loci, and Sole-Cava et al. (1983) were able to distinguish sibling species of *Squatina* (angle sharks) using isozymes. Similarly Naylor (1989) and Lavery (1992) showed that most species of carcharhinid sharks could be distinguished using this technique.

A potentially more powerful approach is to survey nucleotide sequence differences in the mitochondrial genome. Because mitochondrial DNA evolves rapidly, it is possible to distinguish closely-related—as well as distantly-related—species by using either restriction fragment length polymorphism (RFLP) analysis or DNA sequencing. RFLP analysis is an indirect method of DNA sequence analysis that uses restriction enzymes to cleave the molecule at specific 4-,5-, or 6-base recognition sequences. The resultant fragments are size-separated by electrophoresis through agarose or acrylamide gels. Differences in the fragment patterns between individuals provides the basis to assess genetic distinction (Fig. 1). By contrast, with DNA sequencing, it is possible to determine exactly the genetic differences between individuals (Fig. 2).

This paper explores the utility of mtDNA sequence analysis for identifying species of sharks based on information from a study of mitochondrial DNA evolution in sharks (Martin, 1992). A standard protocol has not been developed as a general forensic tool to identify sharks. Instead examples of mtDNA analysis are presented to demonstrate that there are rapid and efficient methods of molecular analysis that permit identification of sharks from small tissue samples.

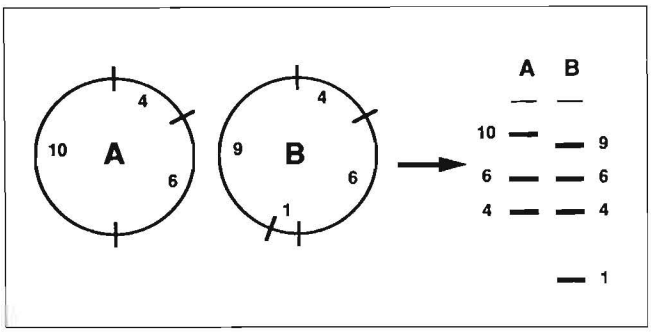

Figure 1

Diagram of RFLP (restriction fragment length polymorphism) analysis. Restriction enzymes cleave the molecule at specific recognition sequences (slash marks) in the mitochondrial genomes (circles) of two species, **A** and **B**, producing fragments of varied sizes (indicated by the numbers). In A there are 3 recognition sites whereas in B there is an additional site, indicating a sequence difference between the two genotypes. The fragments are separated by electrophoresis and the resultant patterns serve as species-specific "fingerprints."

RFLP Analysis of the Mitochondrial Genome

MtDNA is widely used to explore the genetic relationships among individuals because of its maternal inheritance, lack of recombination, ease of purification (Lansman, et al. 1981; Hillis and Moritz, 1990), and rapid rate of evolution (Avise et al., 1987; Moritz et al., 1987) which facilitates distinction of recently diverged species. For example, a typical RFLP study surveys about 400 base pairs. If the average rate of sequence divergence is 0.2-0.4% per million years in sharks (Martin et al., 1992a), then it should be possible to distinguish lineages that diverged as recently as 625,000 to 1,250,000

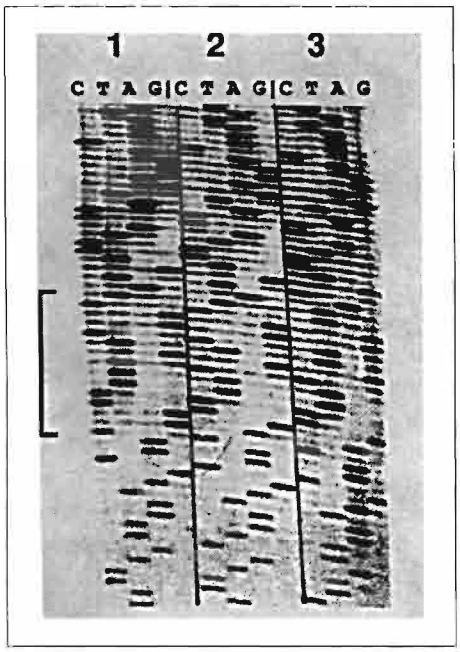

Figure 2

DNA sequencing gel for three species of *Carcharhinus*: 1) *C. longimanus* (oceanic whitetip); 2) *C. sealei* (blackspot shark): and 3) *C. ambionensis* (bigeye shark). For each species there are four lanes (labeled C, T, A, G) corresponding to the four bases. The sequence is read from bottom to the top. For the region bracketed, the sequences (with nucleotide differences in bold face type) for the three species are 1) C**G** GCC TTT GT**C** GG**C** TA; C**A** GCC TT**C** GT**C** GG**C** TA; 3) C**A** GCC T**T**C GTT GGT TA. All of the changes are 3rd codon (silent) position transitions and would therefore be invisible using protein-based methods. Methods for the extraction, amplification, and sequencing of DNA are available in Martin (1992).

years ago. Because substitution rates for nuclear DNA are approximately 10 times slower than for mtDNA (Wilson et al.,1985), similar levels of resolution can be achieved by surveying 40 loci by electrophoresis (Nei, 1985, p. 253).

RFLP analysis of mtDNA has been extremely useful for describing population structure for a wide variety of organisms (Avise et al., 1987) as well as for distinguishing among stocks for fisheries purposes (Ferris and Berg, 1987; Martin et al., 1992b). RFLP analysis of purified whole mtDNA's can reveal diagnostic patterns (Fig. 3) and mtDNA sequence analysis of 16 species of *Carcharhinus* and allied genera shows that morphologically similar species are genetically distinct (Martin, 1992) such that most species can be distinguished using standard RFLP analysis with one or two enzymes.

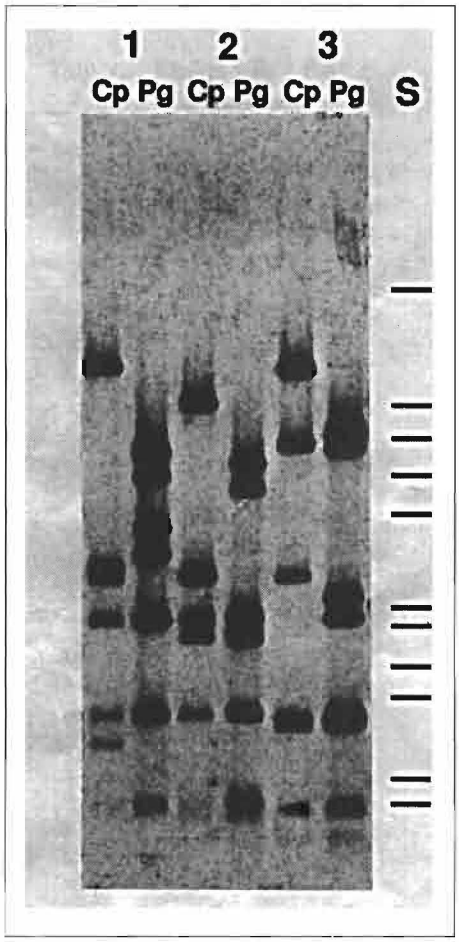

Figure 3

RFLP profiles for *Carcharhinus plumbeus* (CP) and *Prionace glauca* (Pg). For each lane double-digestions were done with *Bcl* I and *Sal* I (1), *Xho* I (2) and *Bgl* II (3). S is a lambda cut with *Hind* III-*Eco* RI for use as a size standard. Fragment sizes (in kilobases) for the lambda size standard are, in order of increasing size (from top to bottom): 21.2, 5.2, 4.9, 4.3, 3.5, 2.0, 1.9, 1.6,, 1.3, 1.0, 0.8. Methods: Purified mtDNA was obtained following the methods of Lansman et al. (1981), i.e., digested with a pair of enzymes following the manufactures guidelines, end-labeled with radioactive nucleotides by using Klenow enzyme, the fragments separated in a 1% TBE agarose gel, the gel dried, and the fragments visualized by exposure to X-ray film overnight.

Enzymatic Amplification and RFLP Analysis

The polymerase chain reaction (PCR) is a technique that enables the amplification of small segments of DNA (Saiki et al., 1988). By using PCR it is possible to retrieve DNA sequences from ancient tissue (Paabo, 1989; Hagelberg and Clegg, 1991) and a range of tissue types preserved by various means (e.g., teeth, jaws, cartilage, fins, dried or salted flesh, blood, preserved museum specimens, as well as from fresh, frozen, or ethanol-preserved samples of liver, heart, kidney, gills, muscle). Protocols have been developed for the isolation and characterization of mtDNA from sharks (Martin, 1992). With sets of conserved primers, different regions of elasmobranch mitochondrial genomes that evolve at remarkably different rates (Cann et al., 1987) (see Fig. 4) can be amplified and subjected to sequence analysis. Specific regions can be chosen to address questions of differing temporal resolution. For example,

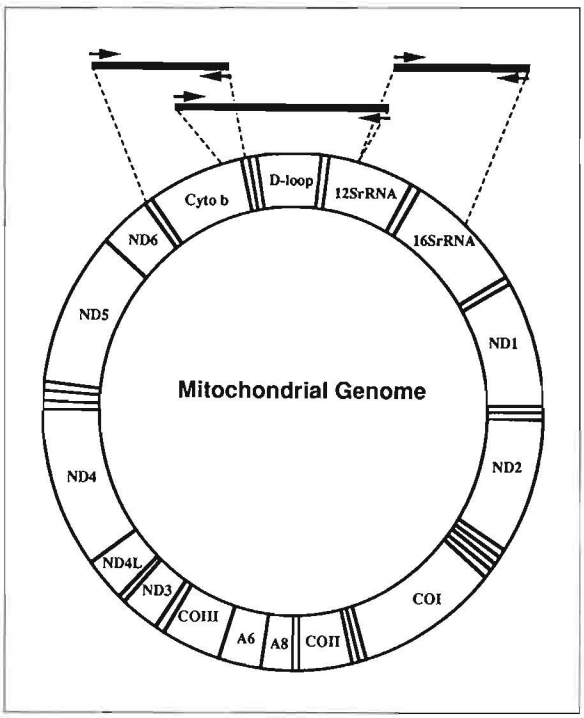

Figure 4

Map of the vertebrate mitochondrial genome (based on mammals and frogs) showing the location of the primers that have been developed to amplify and characterize specific gene regions of elasmobranch mtDNA. For the primer sequences, consult Martin (1992).

the ribosomal genes (12S and 16S) and amino acid replacement positions in the cytochrome b gene evolve relatively slowly (Cann et al., 1987) and are appropriate for distinguishing among relatively distantly related species and genera. By contrast, the non-coding D-loop and 3rd codon (silent) positions in cytochrome b evolve relatively rapidly (Cann et al., 1987), allowing assessment of genetic relationships between closely related species, among populations of a single species, and among individuals within populations.

For distinguishing between species, the size of fragment to amplify and the number of restriction enzymes required depends on the percent sequence difference between species. There are endonucleases that recognize specific 4-base pair (bp) sequences. On average, a specific 4-bp sequence will occur with a probability equal to the product of the frequencies of the 4 nucleotides (G, A, T, and C). For sharks, this value is approximately 0.0024 (Martin, 1992). The expected number of base pairs required for the occurrence of a specific 4-bp sequence is the inverse of this value; thus, for shark mtDNA, there should be a specific 4-bp restriction site every 420 bases. This information allows estimation of how many restriction enzymes are necessary, on average, to distinguish two DNA's of a given size and sequence difference using the formula

$$\text{Number of enzymes} = 1/[4fp(S/420)],$$

where f is the fraction of sites in the DNA molecule that can vary, S is the size of the fragment, and p is the proportion of sites that are different between the two DNA's. For mitochondrial DNA, f is approximately 0.5 (Martin, 1992).

A plot of the estimated number of restriction enzymes required to distinguish DNA's of a given sequence difference versus the size of the amplified DNA (Fig. 5) provides an assessment of the amount of effort required to identify species. The graph indicates that RFLP analysis of small fragments (<500 base pairs) is not likely to be informative and that amplification and RFLP analysis of longer DNA's enhance the probability that two DNA's can be distinguished.

DNA sequence of the cytochrome b genes differs by about 6–10% between many species of *Carcharhinus* (Martin, 1992). Amplification of this gene (about 1200 bp) and digestion with 2 to 4 enzymes should permit discrimination of most species (Fig. 5). When the cytochrome b gene was amplified for eight species and digested with two endonucleases, six distinct haplotypes were identified: four species possessed unique haplotypes and the remaining four species could be separated into two groups (Fig. 6; Table 1). Of course, discrimination between very closely related species (for example, between *C. plumbeus* and *C. altimus* and between *C. longimanus* and *C. obscurus*, species that are only 1.2% and 1.9% different in sequence, respectively [Martin, 1992]), will require amplification and analysis of larger fragments or more than one fragment at a time. The latter can be accomplished by using a technique called multiplex PCR in which multiple sets of primers are included in the amplification reaction to produce multiple products that can be subjected to RFLP analysis.

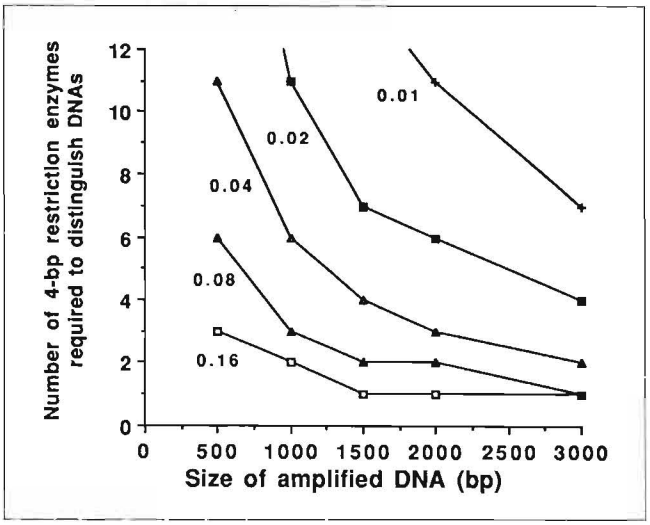

Figure 5

Graph showing the number of restriction enzymes that are required on average, to distinguish two mtDNA sequences of a given level of sequence divergence. The numbers next to the lines are the proportion of sites, p, that differ between two DNA's. See text for explanation.

Table 1

RFLP (restriction fragment length polymorphism) data for the cytochrome b gene amplified by PCR (polymerase chain reaction) and digested with *Hae* III and *Hha* I. Fragments sizes are given in number of base pairs (bp) and are accurate to approximately ±50 bp. ND = not determined. (*C. porosus* appears to be heteroplasmic for two distinct mitochondrial haplotypes.)

Species	Fragment sizes (bp)		Fragment pattern
	Hae III	*Hha* I	
C. amblyrhynchos	1200	1200	a,a
C. falciformis	1000,200	1200	b,a
C. limbatus	1200	1200	a,a
C. obscurus	650, 250, 200	ND	d,?
C. perezi	1000, 200	1200	b,a
C. plumbeus	1000, 200	800, 400	b,b
C. porosus	950, 600, 300, 250,200	700, 500	ef,c
Rhizoprionodon	950, 250	1200	f,a

Before RFLP analysis of PCR-amplified DNA can be adopted as a versatile and efficient forensic tool, it is necessary to determine to what extent, if any, within-species variation in mtDNA sequence decreases the probability that species are accurately identified from small pieces of their mitochondrial genomes. Preliminary analysis indicates that levels of within-species mtDNA sequence diversity are remarkably low (A. Martin, unpubl. data), suggesting that within-species mtDNA diversity will probably not pose a significant problem. Nevertheless, it will be necessary to compile a library of RFLP fragment patterns for each species before the method can be used in forensics.

This technique can also be used to delineate populations (stock structure). The most versatile region to characterize for this fisheries purpose is the non-coding D-loop (see Fig. 4) because this region evolves about 10-20 times faster than the remainder of the genome. As an example, amplification and RFLP analysis of the D-loop and the flanking sequences allows differentiation among hammerhead sharks from different oceans (Fig. 7) and has also been successfully used to describe the population genetics of a North Pacific pelagic marine fish from small muscle samples preserved in ethanol, pieces of frozen liver, and in some cases, from a few eggs less than 1 mm in diameter (Martin et al., 1992). An important advantage of this method is that DNA can be extracted, amplified, digested with endonucleases, and fragment patterns determined for as many as 48 samples in a day; efficiency that permits processing of large numbers of individuals. Furthermore, the same unambiguous data can be obtained regardless of the available tissue type, and the method is relatively insensitive to tissue quality.

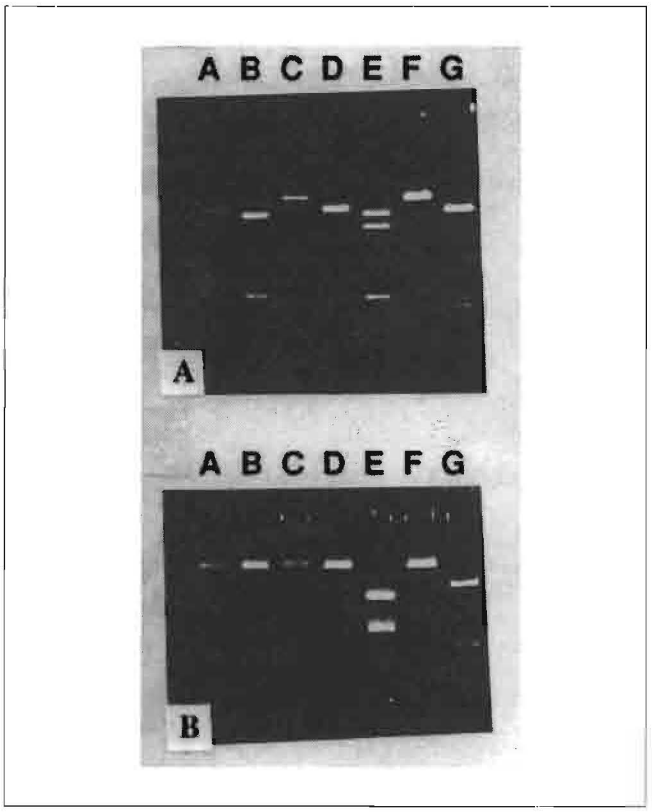

Figure 6

An example of fragment patterns resulting from digestion of PCR-amplified DNA with the 4-base pair endonucleases (**A**) *Hae* III and (**B**) *Hha* I. The DNA was amplified in 100 µL, 15 µL were removed and the enzymes added directly to the amplification cocktail. The sample was allowed to digest for 1–3 hours, 10 µL subject to electrophoresis through a 1.5% agarose gel, and the fragments were visualized with ethidium bromide stain which makes the bands fluorescent when exposed to UV light (see Martin et al., 1992). Fragment sizes are given in Table 1. Lanes: A = *Carcharhinus perezi*; B = *Rhizoprionodon terrenovai*; C = *C. limbatus*; D = *C. falciformis*; E = *C. porosus*; F= *C. amblyrhynchos*; G = *C. plumbeus*.

DNA Sequence Data

DNA sequence provides the greatest resolution of an individual's genotype (see Fig. 2). For studying the genetic relationships among individuals and establishing the genetic difference between individual genomes, there is no substitute (for example, see Vigilant et al., 1991). As part of a larger study on the pattern of diversification in carcharhinid sharks, morphologically similar species of *Carcharhinus* are distinguishable on the

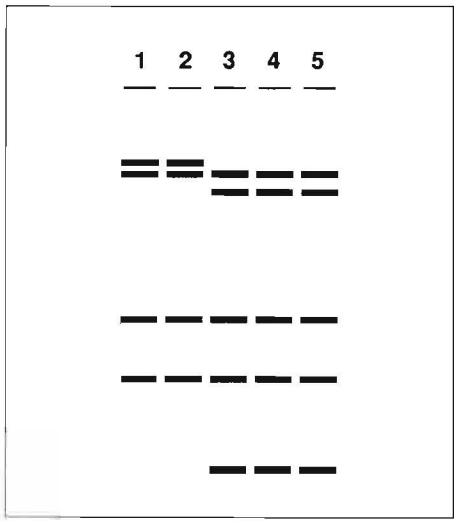

Figure 7

RFLP patterns for hammerheads (*Sphyrna lewini*) collected from five localities. The entire D-loop and flanking gene regions were amplified and digested with *Hae* III directly in the PCR buffer as described in figure 6 legend and in Martin et al. (1992). 1 = Florida keys; 2 = Atlantic coast of Panama; 3 = Hawaii; 4 = Gulf of California; 5 = Pacific coast of Panama.

Table 2

Comparison of various genetic methods of species identification. IEF = isoelectric focusing; RFLP = restriction fragment length polymorphism; and PCR = polymerase chain reaction. Symbols (with scores in parentheses) are as follows: **resolution:** L = low (1), M = medium (2), H = high (3); **tissue type:** S = specific (1), N = non-specific (2); **tissue quality:** S = sensitive (1), I = insensitive (2); **cost:** H = high (1), L = low (2); **ease** or time to determine genotype: S = slow (1), R = rapid (2). The **sum of the scores** allows ranking of the available techniques.

Technique	Resolution	Tissue		Cost	Ease	Sum of the scores
		Type	Quality			
IEF	L	S	S	L	R	8
Allozymes	M-H	S	S	L	R	8
RFLP	M-H	N	S	L	S	8
PCR-RFLP	M-H	N	I	L	R	10
Sequencing	H	N	I	H	S	8

basis of DNA sequences from a small section of the cytochrome b gene (Martin, 1992). However, resolution is not without a price: DNA sequencing is time consuming and relatively costly when compared with RFLP analysis. Thus, for forensic purposes, unless genetic discrimination between very recently diverged (<50,000 years) lineages is required, the cost of this technology outweighs its considerable benefits.

Conclusions

This paper presents a brief sketch of the available techniques for identifying species by using genetic techniques. Table 2 provides a subjective summary of the relative advantages and disadvantages of various technologies. Two things emerge from this table. First, both protein-based and DNA-based methods allow assessment of species identification provided that the necessary library of species' genotypes have been collected. Second, DNA-based technology provides better resolution, does not require specific types of tissue samples to resolve genetic identity, and is less sensitive to the quality of the tissue samples than protein-based methods. Of the five technologies considered in Table 2, RFLP analysis of PCR-amplified DNA shows the greatest promise as a generally applicable forensic tool to aid in the identification and effective management of sharks. However, before this method can be used as a forensic tool, it is necessary to compile a library of fragment pattern "fingerprints" to establish levels of confidence to species identifications made from analyses of DNA.

Acknowledgments

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Shark Conservation — Educating the Public

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ABSTRACT

Current fishing pressure on elasmobranchs has reached levels that are seriously impacting shark populations, and public education regarding the importance of shark resources is essential to timely implementation of appropriate regulatory policy. The primary educational goal of the Monterey Bay Aquarium's temporary (one-year) "Sharks" exhibition and supporting programs was to debunk the popular "Jaws" image while increasing public interest in elasmobranch conservation. About 1.7 million people visited the exhibition and 8,000 participated in associated education programs. Pre- and post-visit interviews revealed changes in visitor attitudes and decreases in misconceptions or mistaken information about sharks as a result of viewing this exhibit. Based on the success of this program, suggestions are made for increasing the interaction between scientists and the public.

Introduction

While insufficient information on elasmobranch life history and fishery characteristics is often cited as reason for the inadequacy of elasmobranch fishing regulations (Anderson and Teshima, 1990; Bonfil et al., 1990; Hoff and Musick, 1990; Pratt and Casey, 1990; Cailliet, 1992), progress is slowly being made toward regulation of elasmobranch fisheries as indicated by the development of the Western North Atlantic Fishery Management Plan (Hoff and Music, 1990; Manire and Gruber, 1990) and recent actions by the California Fish and Game Commission and by other western states (Bedford, 1987; Holts, 1988). It is debatable, however, whether or not adequate management policies can be implemented before some species are significantly impacted (Compagno, 1990; Manire and Gruber, 1990). Timely implementation of elasmobranch fishery regulations may depend as much on changing the public's perception of sharks and on cultivating a conservation ethic, as on attaining much needed life-history information. While conducting research necessary to support management implementation, scientists should also take an active and visible role in public education. Orr (1991) states that the large gap between strong public support for the environment and the environment as a national political issue is partly explained by the failure of scientists to communicate adequately with society. As Kinsman (1991) points out, there is a growing concern about the environment by many outside the environmental and academic circles, however "conservation efforts 'legitimized' by scientists seem distant, and the scientists themselves unapproachable. Part of our responsibility must be to diminish that distance." Interactions between the scientific community and public aquariums and the public education activities undertaken by each group may play an important role in ensuring a timely implementation of much needed management policies.

The Shark Exhibition

In an attempt to increase public interest in elasmobranch conservation, the Monterey Bay Aquarium presented a special "Sharks" exhibition, January through December, 1991, featuring live sharks and a series of interactive exhibits that was augmented by a lecture series, family workshops, a students' art festival, high school and public auditorium programs, and publication of a natural history book. The main theme of the exhibit was that "sharks are not what you think." Subthemes included 1) sharks are not all big and dangerous; 2) sharks are threatened by overfishing and are in

need of conservation; and 3) sharks may play a significant role in regulating prey populations.

The 6000 ft.^{2} exhibit allowed a one-way flow of visitor traffic and focused visitor attention on specific themes as they moved through the exhibit. The "introductory area," with graphic panels, exhibit elements, and a video, addressed visitors' existing attitudes and misconceptions about sharks. Proceeding through the exhibit, visitors encountered 12 species of live sharks (Table 1) in seven tanks ranging in volume from 100 to 3,400 gallons. Accompanying graphic panels explained the varying appearances, adaptations, and lifestyles of the different species. Four interactive exhibits allowed a sensory experience of the relative ways that sharks see, smell, and "feel" (electroreception and lateral line) their environment. The exhibit acknowledged that sharks are predators and demonstrated their adaptations for this role but also illustrated that not all sharks are the big toothy type that popular literature and movies have typically portrayed. Reproductive modes were illustrated by exhibiting three successive phases in the development of live horn shark (*Heterodontus francisci*) and swell shark (*Cephaloscyllium ventriosum*) embryos in their egg cases. Six videos, each at a different location in the exhibit, introduced the themes of each exhibit section, conveyed a conservation stewardship message, and provided in-depth information on the natural history of sharks and their interactions with people. The last video, set in a mini-theater as the visitors' final experience of the exhibit, addressed issues of over-fishing, conservation, management and the need for continued research.

Evaluation Methods of the Shark Exhibit

An evaluation analyzed visitor response to the shark exhibit. The evaluation included, but was not limited to, people's impressions of the shark exhibit, whether the exhibit had informed visitors about sharks, and which exhibit elements informed visitors about sharks. The evaluation investigated cognitive aspects of the visitors' experience (how they perceived the exhibit, what they learned about sharks, their awareness of the messages and themes), and the affective experience (how people felt about the exhibit). The evaluation did not track visitor behavior. The evaluation was designed and conducted by "People, Places & Design Research," Northampton, MA. (The evaluation methods and results are considered proprietary and some specific details are not yet available for publication.)

The research methods for the evaluation involved 1) entrance interviews with 121 visitors before they entered the aquarium, and 2) exit interviews with a separate sample of 375 visitors as they departed from the exhibit. All interviews were conducted between March 13 and April 2, 1991, by aquarium staff with training and guidance from research consultants. Entrance interview questions focused on, but were not limited to: 1) visitors' images and associations with sharks and 2) their knowledge of characteristics shared by most sharks. Exit interview questions focused on, but were not limited to 1) visitors' own assessments of whether they had learned anything new, 2) whether they had changed their attitudes about sharks, 3) their understanding of characteristics shared by most sharks, 4) their awareness of themes in the exhibit, and 5) exhibit elements which prompted that awareness.

Table 1
Live sharks exhibited during the temporary "Sharks Exhibit" at the Monterey Bay Aquarium.

Blacktip reef shark, *Carcharhinus melanopterus*
Bonnethead shark, *Sphryna tiburo*
Brownbanded bamboo shark, *Chiloscyllium punctatum*
Epaulette shark, *Hemiscyllium ocellatum*
Horn shark, *Heterodontus francisci*
Japanese wobbegong, *Orectolobus japonicus*
Leopard shark, *Triakis semifasciata*
Nurse shark, *Ginglymostoma cirratum*
Swell shark, *Cephaloscyllium ventriosum*
White spotted bamboo shark, *Chiloscyllium plagiosum*
Whitetip reef shark, *Triaendon obesus*
Zebra shark, *Stegostoma fasciatum*

Evaluation Results of the Shark Exhibit

Fifty-five percent of the individuals interviewed were first-time visitors to the aquarium and 34% belonged to a nature group. Twenty-four percent of the visitors interviewed were in their 20's, 28% in their 30's, 24% in their 40's, 12% in their 50's and the remainder were over 60 years of age. Forty-seven percent of the visitors interviewed were female and 53% were male. Highlights of the results pertinent to public education and elasmobranch conservation included the following six points:

- Visitors to the aquarium were not completely limited by popular images and they did come with some reasonable information about sharks.
- A majority of visitors (82%) perceived the main theme of the exhibit, that "sharks are not what you think."
- There was good recognition of subthemes in the exhibit, with 67% of the sample spontaneously expressing the idea that sharks are not all big and dangerous, and 43% spontaneously expressing the idea that sharks are threatened by overfishing and are in need of conservation. When asked directly

about these themes, 96% of the visitors recalled seeing the former theme expressed in the exhibit and 86% recalled seeing the latter theme expressed.

- Over 90% of visitors said they learned something about sharks that they did not know before. This included facts about their reproductive process, their sensory abilities, that there are many varieties of sharks in nature, and that some shark populations are decreasing.
- There were strong decreases in misconceptions and misinformation about sharks as well as the addition of new images that were less threatening and more respectful of sharks. For example, the proportion of visitors who responded affirmatively to the question "Do most sharks have big sharp teeth?" was 71% in the pre-visit survey, compared to 23% in the post-visit survey. Similarly, 52% of the pre-visit respondents said most sharks were dangerous and 42% said most sharks were large; in comparison only 14% of the post-visit respondents replied in the affirmative to the same questions.
- Visitor responses in the exit interview indicated that their enhanced understanding and appreciation of sharks resulted from a variety of exhibit elements. When asked what was the most impressive exhibit element, 31% of the visitors answered live sharks, 15% said the reproduction and egg case exhibit and 13% said interaction. Fifty-five percent of the visitors reported that the written signs and labels were a principal source of information about shark characteristics. Forty-seven percent of the visitors said the videos were the most effective element to communicate the message about conservation and preservation, while 39% said that the written signs and labels were most effective.

The Scientist's Role in Elasmobranch Conservation Education

Although the lack of public interest in elasmobranch research, conservation, and management has been attributed to limited awareness and understanding of these topics (Anderson and Teshima, 1990; Compagno, 1990; Manire and Gruber, 1990), the results of this survey indicate that the public is receptive to new information concerning sharks and to the need for shark conservation. Compagno (1990), Manire and Gruber (1990) and others suggested that a concerted effort should be undertaken to increase public awareness of the importance of shark resources and the need for an adequate fishery management policy. Although institutions such as zoos and aquariums usually take the lead role in such activities, cultivating support for elasmobranch conservation is certainly as much the responsibility of the individual scientist.

Because people and the media are fascinated by sharks, the opportunities to educate the public about elasmobranchs are much greater than for many other conservation issues. Scientists should take advantage of this fascination and participate in conservation education by 1) producing lectures and publications for the general public, 2) being available to the media and educational organizations (for interviews, resources, information, etc.), and 3) notifying the media about events involving elasmobranch biology and conservation.

Essential to effectively impacting the management process via public education is that the public be offered a means of taking action. The public can support elasmobranch conservation efforts by 1) writing letters to regulatory agencies and political representatives, 2) changing behaviors which directly impact shark populations (i.e., participation in shark tournaments), 3) providing financial support to appropriate organizations, and 4) furthering their own education and that of others. Scientists interacting with the public and media should include in their repertoire specific details to allow motivated members of the public to pursue action along a number of the avenues listed above.

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A Preliminary Estimate of Natural Mortality of Age-0 Lemon Sharks, *Negaprion brevirostris*

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ABSTRACT

Determination of natural mortality rate is an important step in understanding and quantifying the population dynamics of a species. This is the first study using elasmobranchs which directly measured the rate of natural mortality. An unexploited population of lemon sharks, *Negaprion brevirostris*, in Bimini, Bahamas, was and continues to be censused to determine natural mortality. Preliminary results indicate an instantaneous natural mortality rate (M) ranging from 0.60–1.01 for lemon sharks in their first year of life (equivalent to an annual mortality of as much as 64%). The natural mortality rate must be highest in this age class and must be very low and possibly zero in subsequent age classes for the population to remain viable.

Introduction

There have been few attempts to estimate natural mortality in elasmobranchs. Yokota (1951) estimated the natural mortality of the ray *Dasyatis akajei* to be 0.28 using age composition of an exploited population. Aasen (1963) used length distribution and growth of the porbeagle, *Lamna nasus*, to derive an estimate of M of 0.18 and Grant et al. (1979) used a regression from tag recovery data to estimate a natural mortality rate of 0.10 for exploited stocks of the school shark, *Galeorhinus australis* (= *G. galeus*). For the spiny dogfish, *Squalus acanthias*, Holden (1977) estimated M to be 0.10 based on a length-fecundity relationship, Wood et al. (1979) used simulation data and estimated M to be 0.094 for an equilibrium population, and Jensen (1984) used commercial catch-effort data to derive an M of 0.5. For the little skate, *Raja erinacea*, Waring (1984) used the relationship between the growth parameter K and instantaneous natural mortality as described by Beverton and Holt (1959) to estimate M between 0.4 and 0.5. Finally, for an estimate of natural mortality for the leopard shark, *Triakis semifasciata*, Smith and Abramson (1990) used Hoenig's (1983) regression based on the maximum attained age of a species to estimate M to be 0.14 overall and assumed it was double that in the first year.

Beverton and Holt (1957) believed natural mortality to be the most important parameter affecting the yield curve of a commercial species. Because elasmobranchs are, or are becoming, over-exploited around the world, (Hoff and Musick, 1990; Taniuchi, 1990; and other papers in this report), it becomes increasingly important that estimates of natural mortality of elasmobranchs be made in order to understand their overall rates of production and thus possible potential yields.

Survival data from elasmobranch commercial and sport fisheries are generally unavailable (Hoenig and Gruber, 1990). In a situation where fishing mortality (F) is non-existent, total instantaneous mortality (Z) is equal to the instantaneous rate of natural mortality (M). Therefore, as part of our ongoing study of the population dynamics of the lemon shark (Gruber and Stout, 1983; Brown and Gruber, 1988; Gruber et al., 1988; Cortes and Gruber, 1990), we have undertaken a multi-year field experiment to determine both the natu-

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ral mortality rate and its rate of change over time in the mangrove-fringed Bimini Islands that serve as a nursery area for an unexploited population of young lemon sharks.

Materials and Methods

Study Site

Our study site was the mangrove-lined lagoon area between North and East Bimini, Bahamas, a small chain of islands about 85 km east of Miami, Florida (Fig. 1). Initially we confined this study to the North Sound area (Sites 1–7), but expanded it to include areas southeast of the Sound (Sites 8 and 9) to increase the size of the population under study. The pups occupy these mangrove areas for their first several years of life, each shark occupying a limited home range that increases as the shark grows (Gruber et al., 1988; Morrissey, 1991; Morrissey and Gruber, 1993.).

Sampling Procedure

We used gill nets to census, by way of removal, virtually the entire population of 1990 young-of-the-year (YOY) lemon sharks in the area. We conducted five censuses beginning on July 3, August 25, and November 24 of 1990 and May 24 and June 28, 1991. On each night (set) of the three 1990 censuses, we set 9 monofilament gill nets (90 m × 1 m with 5–7.5 cm mesh) at four sites (Fig.1, [2 nets each at sites 1, 2, and 4 and 3 nets at site 3]) around the North Sound. Beginning with the May 1991 census, we used eight gill nets at four sites (Fig. 1 [2 nets each at sites 1, 4, 8, and 9)]. Nets were set simultaneously between mid and high tide in the late afternoon and were fished for 12 hours into the early morning hours.

During the 12-hour period, each net was continuously monitored. Sharks were carefully removed immediately upon capture and transported to a central holding location. Each shark was weighed to the nearest 10 g,

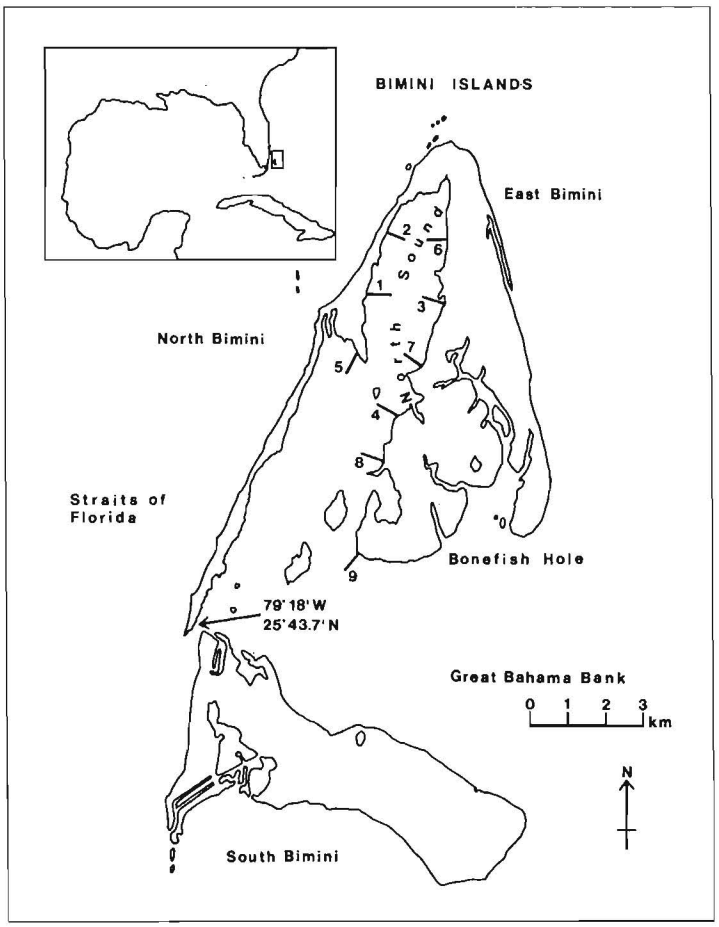

Figure 1
Map of Bimini Islands showing study site and location of gill-net sets. Note: length of gill nets are not to scale. Inset shows relationship of Bimini (in box) to Florida coast.

measured to the nearest 5 mm (precaudal and total length), sexed, scanned for the presence of a Passive Integrated Transponder tag (PIT tag, Destron/IDI Corp.), and externally marked by punching a 4-mm hole in a fin (dorsal, anal, etc.) that represented the site from which the shark was captured. If no PIT tag was found, one was inserted intramuscularly below the first dorsal fin (Manire and Gruber, 1991). Sharks were placed in a holding pen within 15–30 minutes of capture and held there until the census was completed. On one occasion (Census 2–August 1990), we released the sharks from the pen after the second night to determine rate and success of sharks homing back to their site of capture and on the third night censused only the sharks which had not been captured on the two previous nights.

In this paper, we present only data for 1990 young-of-the-year (YOY) lemon sharks. These sharks were easily separable from the other age classes by length-frequency generated during the first two censuses and by tag information thereafter. Analysis of the data for Age 1 and older sharks awaits further sampling experiments.

Population Estimates

Closure was assumed during each removal (census) because 1) each removal experiment was outside the birth period 2) each removal was completed in about 62 hours, during which natural deaths would be negligible and 3) the study population was limited to Age–0 and Age–1 sharks which are highly site attached (Morrissey and Gruber, In press) and thus should not have been moving into or out of the study site.

Several methods are available for estimating population size with removal data. The method of Seber and LeCren (1967) requires only two sampling periods and produces reliable results with a relatively small population if the capture probability during each period exceeds 80% (Seber, 1982). The formula is as follows:

$$N = (u_1^2) \,/\, (u_1 - u_2), \qquad (1)$$

where N = population size,
u_1 = number of captures on first sampling,
u_2 = number of captures on second sampling.

Variance of this estimate can be calculated as

$$\mathrm{Var}(N) = Nq^2(1+q)/p^3 + 2q(1-p^2-q^3)/(p^5-b^2) \qquad (2)$$

where $p = (u_1 - u_2) \,/\, u_1$,
$q = 1 - p$,
and $b = q(1 + q) \,/\, p^3$,

or more simply as

$$\mathrm{Var}(N) = u_1^2 u_2^2 (u_1+u_2) \,/\, (u_1-u_2)^4.$$

We also used a Maximum Likelihood Estimator (computer program CAPTURE [White et al., 1982; Rexstad and Burnham, 1991]) which provides a more precise estimate of population size, sampling variance and a Profile Likelihood Interval (a confidence interval based on the asymptotic χ^2 distribution of the generalized likelihood ratio test [Otis et al., 1978; Rexstad and Burnham, 1991]).

Mortality Estimate

Once a temporal series of population estimates has been made, the total mortality rate can then be calculated. Assuming no births, immigration, emigration, and fishing mortality, any change in abundance must be attributable to natural mortality. It is also assumed that the probability of capture of each individual is the same throughout the population on each capture occasion (Zippin, 1958).

The total instantaneous mortality rate (Z) (Ricker, 1975), is equal to the number of fish, including new recruits, which would die during the year if recruitments exactly balance mortality from day to day. Expressed as a fraction or multiple of the steady density of the stock, this can be calculated as follows:

$$N_t/N_0 = e^{-Zt} \qquad (3)$$

where N_0 = population size at the beginning,
N_t = population size at the end,
t = time (fraction of a year),
and Z = total instantaneous mortality rate.

Actual mortality rate (or annual expectation of death), designated A, which is perhaps a more heuristic measure of mortality, is defined by Ricker (1975) as the fraction of the fish present at the start of a year which actually die during that year. It can be calculated as follows:

$$A = 1 - e^{-Z}. \qquad (4)$$

Further, the survival rate, designated S, can be calculated as follows:

$$S = e^{-Z}. \qquad (5)$$

Survival rate is defined by Ricker (1975) as that fraction of the fish present at the start of a year which will survive for that year.

Results

During five censuses we captured 147 juvenile lemon sharks and tagged 141 of which 36 were 1990 YOY.

None of the sharks in this cohort died during capture or during the 24–72 hours they were held in the pen after capture, and some were captured as many as four times (Table 1).

Census 1 (3–5 July, 1990) consisted of two capture occasions. On the first occasion we captured 43 lemon sharks, of which 26 were Age-0 (1990 YOY). On the second night, we captured 7 sharks of which 3 were Age 0. For these data, the Seber and LeCren (1967) calculation yielded a population estimate of 29 Age-0 sharks (v = 0.70; 95% C.I. = 29–32). This estimate was further confirmed by the fact that we captured only two untagged sharks of this cohort in the next four censuses (12 more sets); therefore, we marked almost 100% of the Age-0 sharks during this first census.

Table 1
Summary of captures during 5 censuses for age class of lemon sharks born in the spring of 1990. Numbers represent sites where sharks were captured. Letters (A, B, and C) represent individual gill-net sets.

	Sets														
	Jul 90		Aug 90			Nov 90		May 91			Jun 91		
Tag ID	A	B	A	B	C	A	B	A	B	C	A	B	C
7F7E296026	2												
7F7E2F1D3A	1		1						1				
7F7E2F1D5E		3											
7F7E2F1F18	4						4						
7F7E2F1F34	4		4					8					
7F7E2F2755	3			4									
7F7E2F2A5B	4												
7F73491968	1		1									1	
7F7E495201	4		4			4							
7F7E49573D	2												
7F734C4B7E	1		1										
7F7E4C4C3	1												
7F7E4C4D23		1											
7F7E4C5578	1		1					1			1		
7F7E4C5F46	4		4					8					
7F7E4C6632	4				4				8		4		
7F734C692B	4		4										
7F7F14410B	3												
7F7F144831	1												
7F7F144832	1			1			1						
7F7F144F73	2				1				1				
7F7F14541D	1		2										
7F7F145458	1		1										
7F7F146320	4			4									
7F7F14645A	3												
7F7F14665E	4												
7F7F152551	4			4				4					
7F7F152556	1			1		1			1				
7F7F3F3C08		1					1						
7F7F197726			1			2			1				
Totals	26	3	11	6	0	3	1	6	3	1	4	1	1

To verify that we had sampled the entire North Sound population, we sampled two additional sites inside the North Sound (Fig. 1 [sites 6, 7]), as well as two sites just outside the Sound (Fig. 1 [sites 5, 8]), before releasing the penned sharks. We captured only one additional shark within the Sound (it was older than Age-0). In contrast, we captured and tagged five Age-0 lemon sharks outside the Sound. None of these 5 were recaptured inside the Sound until May, 1991, at Age 1 when we captured one (originally tagged at site 8) at the adjacent site 4. Further, none of the 29 captured inside the North Sound were captured outside the Sound until May, 1991, when three (all tagged at site 4) were captured at Site 8 (Table 1). This demonstrated to us that we were effectively sampling the entire North Sound area and the study population was highly site-attached in that area (Morrissey and Gruber, 1993.).

The second census took place 25–28 August 1990, at the same four sites as census 1. Our capture rate was somewhat lower than the first census (Table 1) so we added a third night to this and subsequent censuses. These data yielded a population estimate of 17 (v = 0.69) giving a Profile Likelihood Interval of 17–20.

The third census took place 24–26 November 1990. In two nights of gill-net sets, we captured only nine lemon sharks of which four were Age 0. This census was terminated prior to completion because the gill nets were apparently not fishing efficiently in the cold water and the sample size was not adequate to estimate population size.

Census 4 and Census 5 included a larger area (and population) than the three previous censuses. We used the two net sites in the North Sound (Fig. 1 [sites 1 and 4]) where 80% of captures were taken in the first two censuses and added two sites southeast of the Sound (sites 8 and 9). Of the sharks taken from the two discontinued sites (2 and 3), 60% overall and 50% (n = 4) of this cohort were captured at sites 1 or 4 on other occasions. Of the other 4 of this cohort tagged at sites 2 and 3, none were ever captured at any other site and had assumedly suffered mortality. We captured 10 of the previously tagged (1990 YOY) sharks, now Age 1, on the three sets of Census 4 (24–27 May 1991). This yielded a population estimate of 10 (v = 0.86) and a Profile Likelihood Interval of 10–17. During census 5, 28 June–1 July 1991, we recaptured six sharks from the 1990 YOY population. This capture rate yielded a population estimate of 6, (v = 0.67) and a Profile Likelihood Interval of 6–14. However, three of the six had not been captured during the previous census.

Using the data of Table 1, we can be certain of the following population estimates:

- July 1990 Census — 30 of 1990 YOY present in North Sound,
- Aug 1990 — at least 20 of 1990 YOY present, and

- May 1991 — at least 13 of 1990 YOY present.

We calculated several estimates of natural mortality. Based on the July 1990 estimate of 30 sharks (as modified to account for the one untagged capture of Aug 1990) coupled to the May and June 1991 data of 13 sharks, we calculated a mortality rate for the first year of life of lemon sharks:

Total instantaneous mortality rate (Z) = 0.94
Actual mortality rate (A) = 0.61
Survival rate (S) = 0.39.

Using the maximum estimate for census 1 (32 sharks) and the minimum of 13 sharks for the May 1991 census, we yielded estimates of

$$Z_{max} = 1.01,\ A_{max} = 0.64,\ S_{min} = 0.36.$$

Likewise, the minimum mortality rate was calculated by using the minimum population estimate of census 1 (29 sharks) and the maximum population estimate of census 4 (17 sharks). This yielded minimum estimates of

$$Z_{min} = 0.60,\ A_{min} = 0.44,\ S_{max} = 0.56.$$

Discussion

Several factors make this population of sharks suitable for the determination of natural mortality. First, the juvenile lemon sharks are virtually unexploited. Second, a high degree of site attachment by individuals (Gruber et al., 1988; Morrissey and Gruber, 1993) and the relative isolation of the juvenile population provide a situation similar to that of freshwater lakes. Because of this, we assumed a closed population, ideal for the determination of natural mortality.

One disadvantage of the census was the small population size, numbering less than 100. This small size and slow individual growth prohibited the use of length-frequency analysis to estimate mortality of age classes.

Removal methods reliably and accurately estimate abundance as long as a large portion of that population is removed on each sampling occasion (Seber and LeCren, 1967; Seber, 1982). The removal model assumes closure during the censusing period, i.e., no births or deaths and no immigration or emigration. While the assumption of complete closure cannot be completely verified in an open marine ecosystem, a close approximation to the complete closure assumption must be made (Seber, 1982) and is made here.

Hoenig and Gruber (1990) estimated first-year survivability of sharks under a variety of scenarios to range from 16 to 97%. Our calculated survivability of 39% falls below the 50% estimate used for most of Hoenig and Gruber's (1990) calculations, but equals the minimum rate Hoenig and Gruber (1990) estimated for an unexploited population to maintain equilibrium. These estimates suggest that the Bimini population is near equilibrium and is therefore highly vulnerable to exploitation.

Equal mortality for all age classes is believed to be the case for some long-lived teleosts (Seber, 1982) and has been assumed in elasmobranch studies (Wood et al., 1979), but our findings indicate that this is not the case with this population. According to our study, juvenile lemon sharks experience a very high mortality rate during their first year, probably due to predation from large sharks (Branstetter, 1990; Cortes and Gruber, 1990) in the first few months of life.

One important fact has emerged during this preliminary portion of this study: some of the 1990 YOY population had avoided capture during Censuses 2 or 4, or during both, and were later captured, thereby calling into question our assumption of equal probability of capture. Possible reasons for the invalidity of the equal probability of capture assumption include immigration and emigration from the study site or subsequent avoidance of the net by learning processes. We believe the latter explanation to be more likely for two reasons. First, the high degree of site attachment noted in Table 1 and the fact that none of this cohort were ever captured beyond site 8 makes migration highly unlikely. Second, the capture probability of our study population on their first exposure to a gill net was 84% per set in July, 1990, whereas by May, 1991, it had decreased to about 38% (5 of 13) of the documentable population. However, the capture probability in May, 1991, for the new age class not previously exposed to gill nets was 80%. During this study, we observed that juvenile lemon sharks from this and other populations became progressively more difficult to capture in nets with repeated capture attempts and this could artificially inflate mortality estimates.

Abundance estimates must account for learning processes and other behavioral biases. Although White et al. (1982) recommended the use of a behavioral bias estimator ($M(b)$) of Zippin (1958), this method uses only first captures to estimate the total population size at each census. However, because we captured nearly 100% of the population each census, there were insufficient new captures after the first census, which precluded the use of this estimator. We hope to minimize the behavioral bias in the future by sampling the population only once annually (so as to preclude repetitive learning processes) and by baiting sharks to the nets (to increase our capture rate).

Because of these potential biases in our data we must emphasize that these are preliminary results. All noted

biases would cause an overestimate of the natural mortality rate and therefore the actual natural mortality probably lies between our calculated estimate and our minimum estimate ($0.94 > M > 0.60$). This translates to an annual mortality rate of 44–61%. In any case, this remains a high mortality for a single age class of sharks.

Holden (1972, 1974–1977) warned of the difficulty that arises from elasmobrahcn exploition. Our results suggest the potential vulnerability of a stock to over-exploitation may be even more extreme than Holden believed.

Acknowledgments

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Biological Parameters of Commercially Exploited Silky Sharks, *Carcharhinus falciformis*, from the Campeche Bank, Mexico.

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ABSTRACT

Age, growth, and reproductive parameters were estimated for silky sharks (*Carcharhinus falciformis*) off the Yucatan peninsula, Mexico, as a first and essential step towards the assessment and management of the species. Commercial catches were sampled from March 1985 to August 1989. Silky sharks off Yucatan are born in early summer after a 12 month gestation period at c. 76 cm TL. Males mature at 225 cm TL (≈10 y) and females at 232–245 cm TL (>12+ y). Maximum ages determined by analysis of alizarin-red-S-stained thin vertebral sections, were 22+ yr for females and 20+ yr for males. No differences in growth between the sexes were detected. Individual growth is quite variable in this species, but the von Bertalanffy model adequately described population growth. Parameters estimates of this model for combined sexes were: k = 0.101, L_{inf}= 311 cm TL and t_0= -2.718. Age and growth determinations are supported by back-calculation and length frequency analysis. Present results are compared with those of previous studies for this species, and future work for Gulf of Mexico populations is proposed.

Introduction

The silky shark, *Carcharhinus falciformis* (Bibron), is a large, pantropical species attaining 330 cm TL (Garrick et al., 1964) that inhabits both coastal and oceanic waters. Fisheries for this species probably exist worldwide (Compagno, 1984). In southeast Mexico, the silky shark represents one of the more important species in the Yucatan shark fishery (Bonfil, 1987), and it is also exploited commercially along the rest of the Gulf of Mexico and on the Pacific coast of Mexico.

Worldwide there have been very few studies concerning silky shark biology. This has hindered studies of its potential for exploitation. Various discrete accounts of its biology are known thanks to its regular presence as bycatch on tuna, billfish, and other fisheries (Strasburg, 1958; Springer, 1960; Guitart-Manday, 1975). Apart from the studies of the uterus and placentation made by Gilbert and Schlernitzauer (1965, 1966), specific records of reproduction in this species are limited to the scattered field observations of, among others, Strasburg (1958), Springer (1960), Bane (1966), Bass et al. (1973), Stevens (1984, a and b), and Branstetter (1987), with the latter providing the most updated and comprehensive account. Schwartz (1983) reported limited data on its age and growth, and Branstetter and McEachran (1986) and Branstetter (1987) estimated the age and growth of populations in the Northwest Gulf of Mexico.

In Mexico, no specific studies on the biology of this species have been published. Only species accounts (Castro-Aguirre, 1967; Applegate et al., 1979) and its importance and structure in the commercial fisheries (Bonfil, 1987; Bonfil et al., 1988, 1990) have been reported. The present study analyzes the information gathered in almost five years of sampling commercial catches, and aims to estimate reproductive parameters and the age and growth of the silky shark, *Carcharhinus falciformis*, from the Campeche Bank, Mexico.

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Methods

All data were collected between March 1985 and August 1989, at the major commercial fishing ports of Yucatan, both onboard fishing vessels waiting to land their catches, and at nearby processing plants. Some limited sampling was also done during shark fishing research cruises made on I.N.P. (National Institute of Fisheries) RV *BIP III* and RV *BIP X*. All fishing operations took place on the Campeche Bank (Fig. 1). A total of 837 silky sharks were sexed and measured as recommended by Compagno (1984), i.e., with the shark lying on its belly and the upper caudal fin in line with the body axis; total lengths by other methods produce slightly shorter figures. Measurements, taken to the shortest centimetre were total length (TL), fork length (FL), precaudal length (PL), and the length from the tip of the snout to the beginning of the second dorsal fin (DL). Morphometric equations were derived (Table 1), and used to calculate total lengths when sharks were landed with their caudal fins removed.

Internal inspection of the specimens to determine maturity was seldom possible because of restrictions imposed by the handling and processing requirements of shark owners. We could only internally examine sharks when they were being processed. Only external characteristics were used for the determination of sexual maturity in males. Following Springer (1960) and Clark and von Schmidt (1965), males were considered fully mature when the claspers were completely calcified and the distal cartilages of the clasper could be spread open. Additionally, the presence of haematose spots in some male claspers, indicating recent copulation, served as confirmation of sexual maturity. Clasper lengths were

Table 1
Numerical relationships between different lengths of silky sharks from Yucatan (sexes combined). (TL= Total Length, FL= Fork Length, PL= Precaudal Length, DL= Length to beginning of 2nd dorsal fin, n= sample size; r = correlation coefficient.)

Equation	n	r
PL= 1.1505 + 1.1443 DL	196	0.999
FL= 2.8007 + 1.2305 DL	192	0.998
TL= 5.3314 + 1.5275 DL	145	0.997
FL= 1.3017 + 1.0758 PL	292	0.999
TL= 3.4378 + 1.3358 PL	283	0.997
TL= 1.8878 + 1.2412 FL	280	0.997

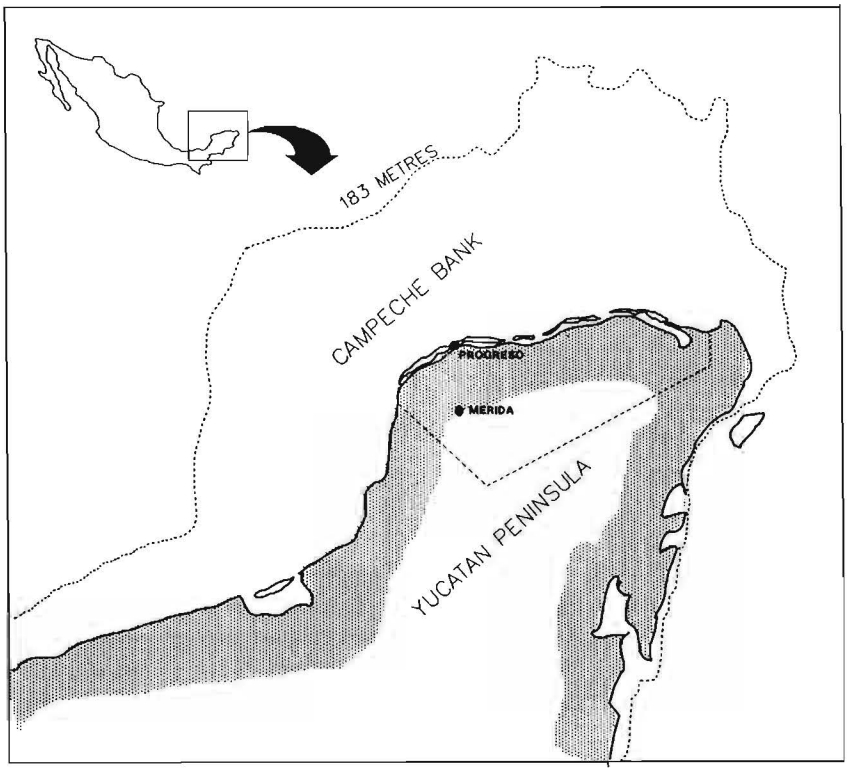

Figure 1
Peninsula of Yucatan, and Campeche Bank, showing the 100-fm isobath.

measured from the insertion of the inner corner of the pelvic fin to the distal tip of the clasper to the shortest millimetre. Given the distinct process of clasper development common to many shark species (Gilbert and Heath, 1972; Parsons, 1983; Natanson and Cailliet, 1986; Peres and Vooren, 1991), clasper length as a percentage of total length was plotted against total length in order to estimate the minimum size at which all males were mature. Pratt (1979) noted that external features can be misleading regarding sexual maturity for female sharks. Therefore, female maturity estimates were restricted to those fish examined at the processing plants. Females were considered mature if ripe ovarian eggs or embryos were present, or if distention of the uterus showed evidence of prior pregnancy. Whenever pregnant females were examined, all embryos in the litter were measured and sexed.

For age and growth studies, a sample of 4 or 5 vertebrae were removed from the region directly below the first dorsal fin for a total of 83 *Carcharhinus falciformis* of both sexes (43♂, 40♀), from newborn to adult sharks, found in the Campeche Bank. Each sample was fixed in 10% formalin for 24 hours, and stored in 70% isopropanol for up to 4 years. For the preparation of the thin sections, one vertebra from the sample was selected, and excessive connective tissue and vertebral processes were removed. Cleaned centra were placed in 50% bleach for periods varying from 5 minutes to several hours, depending on the size of the vertebrae; the larger ones required up to 6 hours and one or two changes of bleach solution. This treatment cleaned most of the unwanted connective tissue remaining on the face and around the centra (Cailliet et al., 1983). Care was taken not to leave samples in the bleach solution too long as this can soften and deform the whole centra. Afterwards, all centra were thoroughly rinsed in running tap water. Cleaned centra were cut in half across a frontal plane using an Isomet low speed saw. A thin (ca. 0.21 mm) slice was obtained from one of these halves by using the same cutting tool, thus a bow-tie shaped section was obtained for each centra.

Two staining techniques were tested on twin sets of 6 vertebrae of different sizes. First, an adaptation of the technique shown by Stevens (1975) was used. This consisted of immersion in a solution of silver nitrate (1%) coupled with exposure to UV light (direct sunlight) for 1–5 min, followed by removal of excess silver and by fixation with soaking in sodium thiosulphate (5%) for a couple of minutes. The second group of vertebrae were stained in an aqueous solution of alizarin red S and 0.1% NaOH in a ratio of 1:9 (Gruber and Stout, 1983) for periods varying between 20 minutes and 4 hours according to the centra sizes, larger ones taking more time. The samples were then rinsed for 15 minutes in running tap water and fixed in a solution of 3% hydrogen peroxide. All stained vertebrae were finally rinsed in tap water and stored back in isopropyl alcohol.

Throughout this paper, we follow the definitions of Wilson et al. (1983), according to which "an annulus is a concentric zone, band or mark, that is either a ridge or valley, or translucent or opaque. A unit passage time (i.e. 1 year) is not inherently implied." The terms band, ring, mark, or zone are regarded by the above mentioned authors as auxiliary descriptive terms. Following Cailliet et al. (1983), rings are treated here as the narrowest kind of concentric mark observed, and bands as wider concentric marks composed of groups of rings. Counts and measures of growth bands were performed on the thin sections viewed at 5× magnification under a binocular microscope equipped with an eyepiece micrometer. The centra faces were used only as an aid for identifying and counting poorly defined bands in the corpus calcareum and intermedialia. Both transmitted and reflected light were used to examine the samples depending on the quality of the definition of the growth marks. To increase contrast of the growth marks, transmitted light surrounding the sections was sometimes partially blocked by inserting suitable pieces of common writing paper between the container and the microscope platform.

Two separate counts were made by a single reader (senior author) for each sample, without knowledge of the total length or sex of the shark. When the two counts differed, a third reading produced a count that matched one of the first two. Agreeing counts were used in the calculation of the mean length at age for each age class.

The centrum radius was measured as a perpendicular line from the focus to the most distal edge of the vertebrae, which usually lay in the corpus calcareum. Distances to each growth mark were also measured as perpendicular lines from the focus to the most distal point of each growth mark along the corpus calcareum (Fig. 2). Marginal increments were measured perpendicularly from the last growth mark to the edge of the centrum. Birth marks were identified as a change in the angle of the inner margin of the corpus calcareum; this was sometimes coupled with a faint narrow annulus traversing the intermedialia. In most cases this annulus was proximal to the angle change.

Back-calculated lengths were derived from the vertebral radius-total length regression equation. The Dahl-Lea method (Casey et al., 1985; Branstetter, 1987) was also used, but discarded as it did not adequately describe early growth compared with the regression method. Care was taken to assign correct ages to the mean lengths-at-age as these can be different for direct vertebrae readings (length at time of capture) and back-calculated data (length at annuli formation).

With a maximum likelihood computer program (Genstat5), von Bertalanffy growth curves were fitted

to the mean lengths at age obtained from the vertebral readings, as well as for those obtained via back calculation. Whenever necessary, comparisons between growth curves were performed using a computer-generated parallel curve analysis of covariance (Genstat5). Unless otherwise stated, all statistical analyses were performed using $\alpha = 0.05$.

Verification of the growth estimated from vertebrae was done using length-frequency data for 738 free-living silky sharks. These data were analyzed by Shepherd's method (Shepherd, 1987) with the LFDA (Length Frequency Data Analysis) package. Given the ability of this program to run alternatively with a single set of length-frequency data (LFD), or with a collection of time-related sets of data (Jones et al.[1]), runs were performed on monthly LFD sets available within each year (designated "partitioned" analyses), as well as on single yearly sets and on the pooled database (designated "summarized" analyses).

[1] Jones, C. G., M. Basson, and S. Holden. 1989. L.F.D.A. length frequeny data analysis. A prototype software package for the estimation of growth parameters from length-frequency distributions. Renewable Resources Assessment Group and Overseas Development Admin., unpubl. manuscr., 46 p.

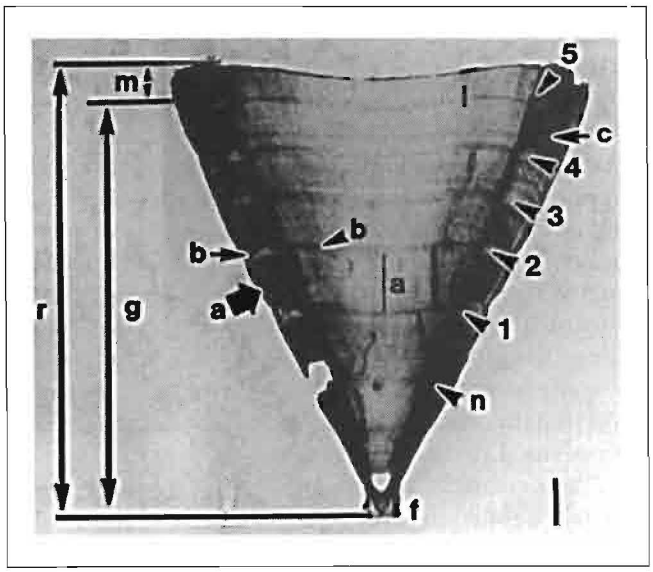

Figure 2
Bow-tie thin section of a 199-cm TL male *C. falciformis* alizarin-red-S stained vertebral centra with 5+ growth bands. The method used to measure the radius (r), marginal increment (m), and distance to a growth mark (g) is indicated, along with the broad "summer" annuli (a), the narrow "winter" annuli (b), the focus (f), birth mark (n), corpus calcareum (c) and intermedialia (i). Scale = 1 mm.

Results

A total of 738 freeliving silky sharks were analyzed (Fig. 3). The 352 males ranged from 69–314 cm TL, whereas females ranged from 65–308 cm TL. An additional 99 embryos ranging from 25 cm to 77 cm TL were examined.

Reproduction

Data on clasper length from 132 silky sharks showed mature males measure from 216 cm TL onwards, but some immature sharks were still found at 220+ cm TL. Fitting a Gompertz curve to the data (Fig. 4) indicated that 225 cm TL generally separated fully mature individuals from those with undeveloped or developing claspers. Taking 314 cm as the maximum total length observed for males in the Campeche Bank (present data), maturity is attained at 72% of the maximum length.

For female *Carcharhinus falciformis*, the limited data allowed only a rough reconstruction of a size range at first maturity. The smallest of 13 pregnant females examined were two specimens of 246 cm TL. Otherwise, mating bites which suggested maturity were observed on three females of 232 cm, 235 cm, and 241 cm TL. This range corresponds to 75–78% of the maximum total length observed in this study (308 cm).

Length-frequency distributions of late embryos and newborn sharks indicated a size at birth of c. 76 cm TL (Fig. 5). The smallest free-swimming shark was 65 cm TL, and the largest embryo was 77 cm TL.

Changes of mean total length of embryos in 13 litters indicated summer was the birth season and there was an approximate one-year gestation period (Fig. 6). A clear trend of embryonic development from September to July was found, and full-term embryos present from May through July. No embryos were recorded during August. For further calculations in this study, the month of July was set as the time of birth for silky sharks in the Campeche Bank. Assuming that mating takes place in late spring (Branstetter, 1987), an approximate 12-month gestation period can be derived from the present data.

Litter size varied between 2 and 12 embryos. Because of the fact that embryos are sometimes aborted by females trying to escape from the fishing gear, or may be expelled from the dead mother's belly during handling operations, this lower limit may be an underestimate. The sex ratio of 99 embryos was 1:1.17 (males:females). All free-living silky sharks (n=738) had a sex ratio of 1:1.10, while pre-adult and adult sharks (those larger than 200 cm TL; n=211) had a 1:1.37 sex ratio.

Age and Growth

The success of the two staining techniques was variable. Although silver nitrate staining yielded alternate brown-

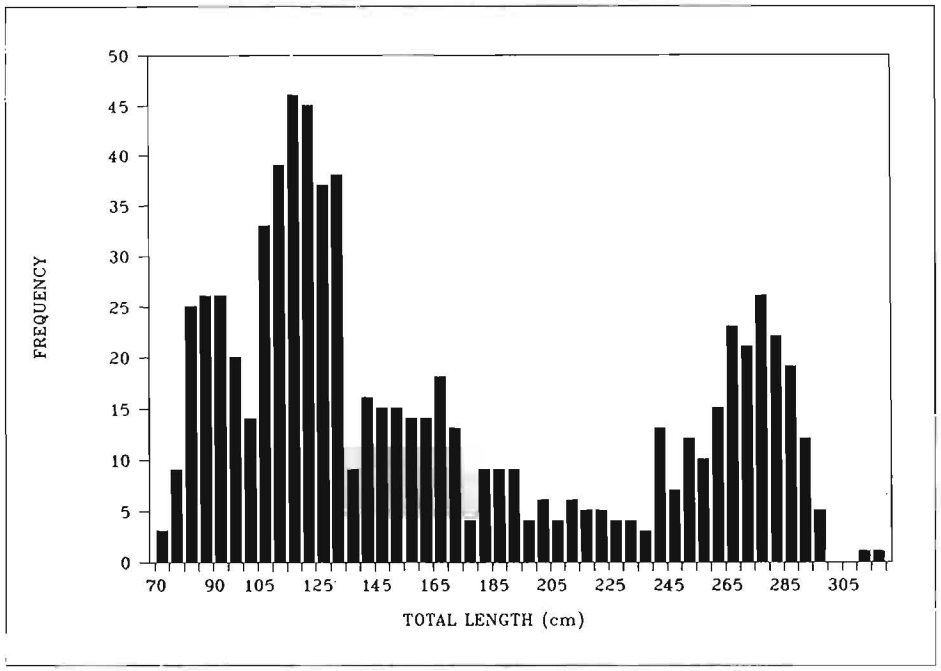

Figure 3
Length-frequency data set of the 738 freeliving sharks analyzed in the study, and used as one of the summarized data sets in the LFD analysis.

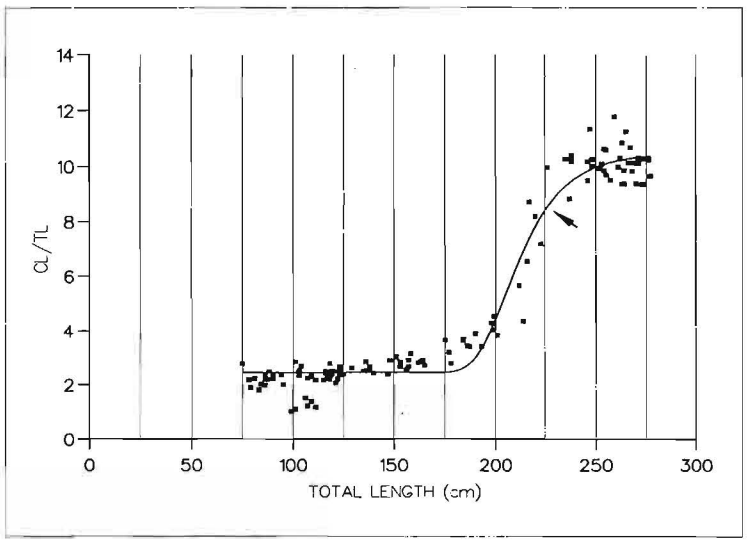

Figure 4
Estimation of size at first sexual maturity for male silky shark, based on the relative development of clasper length with total length. Squares are observations, arrow shows approximate size at which all sharks are mature.

ish and blackish bands on centra faces, poor differentiation was obtained on the exposed frontral-cut surfaces of the centra halves and the thin sections. In contrast, alizarin-red-S stained vertebrae provided a more consistent differentiation of the banding pattern throughout the centrum faces, frontal-cut surfaces, and thin sections. For this reason, and because of the ease of the alizarin-red-S method, this method was adopted for all samples.

In the corpus calcareum of a typical centrum section there was a clear pattern of annuli pairs composed of a broad dark purple band followed by a narrower light

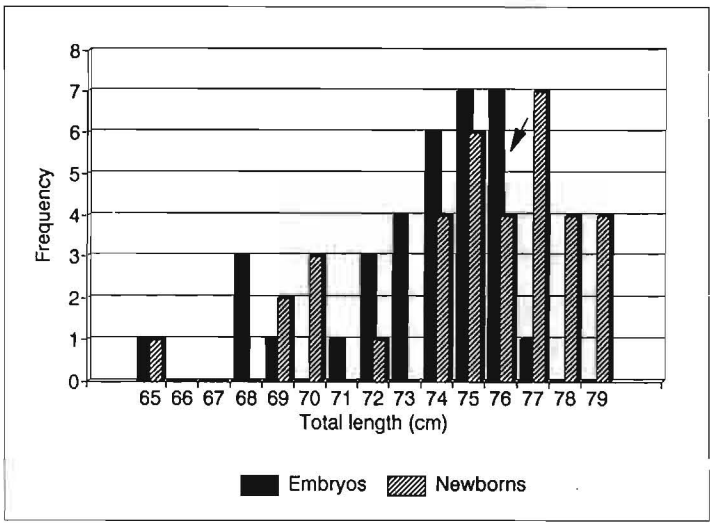

Figure 5
Estimation of size at birth (pointed by an arrow) for *Carcharhinus falciformis* from length frequencies of full term embryos and newborn sharks.

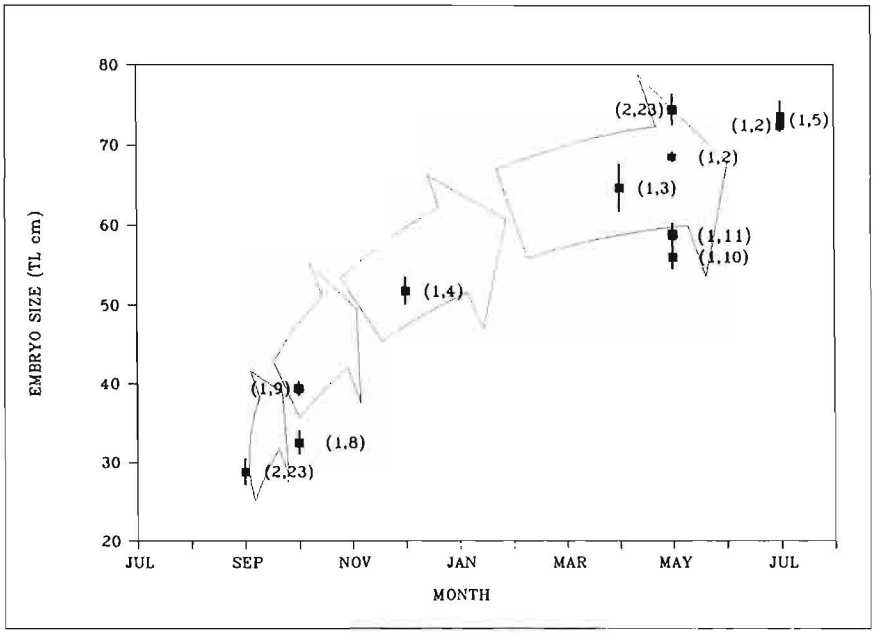

Figure 6
Development of silky shark embryos through time. Numbers in parentheses represent number of litters and total number of embryos. Squares are mean values; vertical lines are one standard deviation.

purple or white band. The broad annuli of the corpus calcareum corresponded to broad bands of narrowly spaced rings in the intermedialia, and the narrow translucent band corresponded to still narrower very dark rings (Fig. 2). The first 5–10 pairs of annuli were generally very broad in a section but consistently changed into very narrow pairs afterwards. Annulus counts after two separate readings agreed 45% of the time, 31% of the readings differed by one annulus, and 24% by more than one.

A significant linear relationship (α=0.0005) was found between the vertebral radius and total lengths of silky sharks (Fig. 7). Marginal increments increased during the calendar year with a maximum in December and a

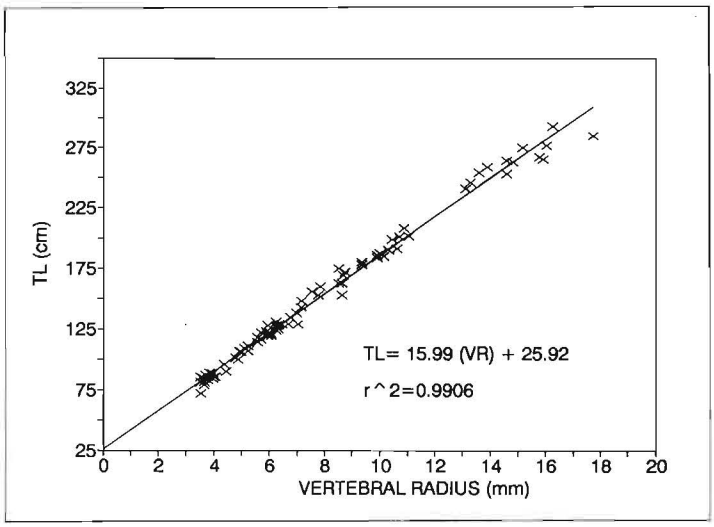

Figure 7
Linear relationship between vertebral radius and total length for silky sharks of the Campeche Bank.

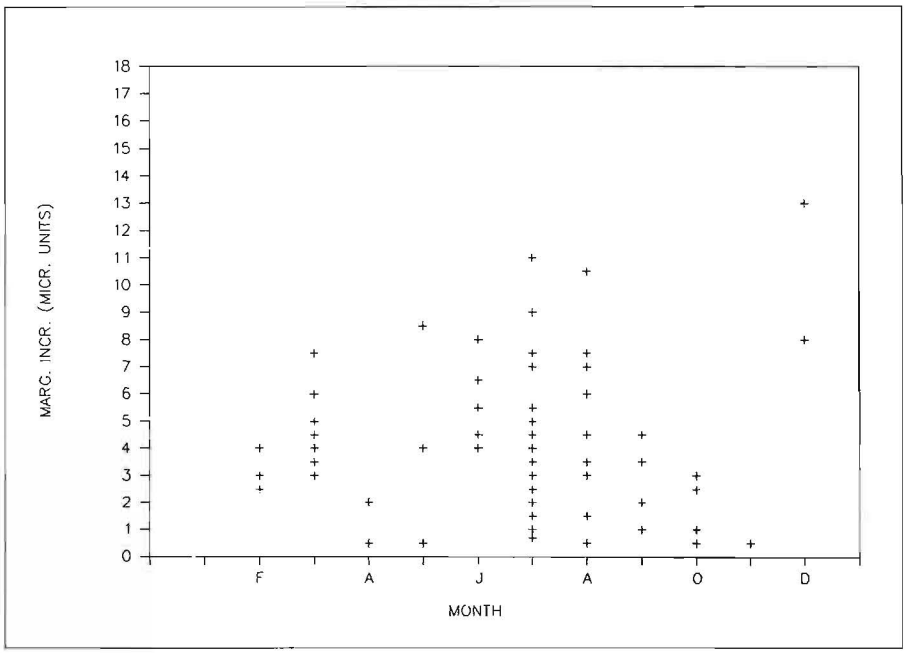

Figure 8
Estimation of time of annulus formation in centra of silky sharks based on the analysis of marginal increments for each month (neonates without winter mark excluded).

minimum in February (Fig. 8). Accordingly annulus formation occurred sometime between August and December. For growth calculations, December 30 was taken as the date of annulus formation.

With a July birth for silky sharks on the Campeche Bank and a December annulus formation, the first winter annulus represents only 6 months of growth; subsequent annuli formed annually. This was supported by the fact that mean growth represented by this first band was 13 cm, about half the average growth observed from the first to the second winter annulus (20 cm).

Fits of the von Bertalanffy Growth Model (VBGM) to the observed data for each sex provided values of k = 0.091, L_{inf} = 314.9 cm TL, and t_0 = –3.18 yr for females,

and k = 0.098, L_{inf} =301 cm TL, and t_0 = –3.05 yr for males. Comparison of the two curves showed no significant differences in growth for males and females of *Carcharhinus falciformis*. Therefore, data for both sexes were combined and used to fit the VBGM to them (Fig. 9). Growth parameters for combined data were k = 0.089, L_{inf} = 313.1 cm TL, and t_0 = –3.3 yr.

The back calculations supported direct readings (Table 2). For these comparisons it must be noted that observed data should be greater than back calculations, as the former are based upon lengths at capture, whereas back calculations are based on lengths at band formation. The von Bertalanffy growth curve fitted to back-calculated mean lengths at age was not significantly different from that obtained for the direct readings (Fig. 9). Given the greater number of data taken into account for the back-calculated curve, parameters derived from this analysis were adopted as the ones best describing growth for silky sharks in the Campeche Bank. These values were k = 0.101 ,L_{inf}=311 cm TL, and t_0 = –2.718 yr. Analysis of the back-calculated mean lengths at age showed that strong variations in growth occurred between year classes in *Carcharhinus falciformis*, but overall, no Rosa-Lee phenomenon was detected (Fig. 10).

Back calculations illustrated that, on average, silky sharks in the Campeche Bank grew about 13 cm in their first 6 months of life, c. 19 cm/yr during the following 3 years, c. 15 cm/yr in the next 3 years, c. 11 cm/yr for the next 4 years, and finally c. 6 cm/yr or less for the rest of their life. According to the growth parameters adopted, and the lengths at maturity found for the species in the Campeche Bank, the age at maturity for males in the area is 10 yr, whereas for females it is 12+ years.

Analysis of length-frequency data with the LFDA program produced varying VBGM parameter estimates (Table 3). The growth parameter k varied between 0.085 and 0.13, L_{inf} from 298–365, and t_0 from 0.22–0.97. The overall range of results agreed well with those obtained by the vertebrae study especially for the growth parameter k. The averages of the VBGM parameters obtained from all successful runs of the program (k = 0.101, L_{inf} = 320 cm TL, and t_0 = 0.76 yr) provided good evidence for verification of the direct determination of growth in the silky sharks of the Campeche Bank.

Discussion

Reproduction

Few estimates of reproductive parameters are available for the silky shark; nevertheless, available data suggests a much smaller size at maturity for females in the Indian and Pacific Oceans compared with those in the Atlantic. In the western Indian Ocean, Bass et al. (1973) complemented observations on nine silky sharks with Fourmanoir's (1961) data, and found a larger size at birth (78–87 cm TL) and mature specimens of both sexes at larger total lengths (males at 240 cm TL, females at 248–260 cm TL) than those obtained by us. In approximately the same area (Aldabra Atoll), Stevens

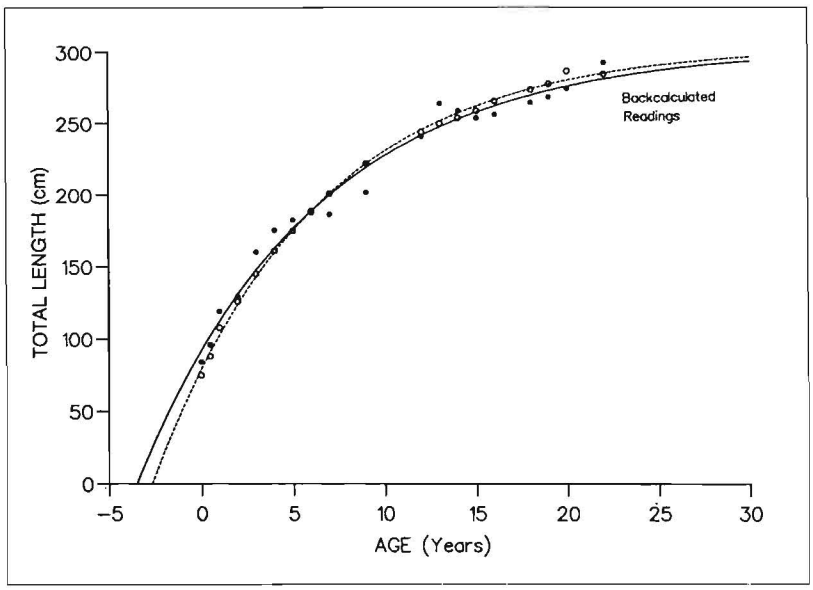

Figure 9
Von Bertalanffy growth curves fitted to mean lengths at age from direct vertebrae readings (dots), and back-calculation (circles) for *Carcharhinus falciformis*.

Table 2
Back calculated mean total lengths-at-age for silky sharks from the Campeche Bank (cm).

		Growth marks																						
		0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Age class	*n*	0	0+	1+	2+	3+	4+	5+	6+	7+	8+	9+	10+	11+	12+	13+	14+	15+	16+	17+	18+	19+	20+	21+	22+
Birth	15	76																							
1	6	74	88																						
2	16	74	87	109																					
3	11	74	85	100	118																				
4	5	75	92	108	128	149																			
5	4	77	94	114	135	149	162																		
6	4	75	85	107	124	141	156	172																	
7	5	76	87	107	119	134	146	159	174																
8	3	74	90	106	117	130	141	155	167	181															
10	1	67	80	108	133	143	156	164	172	181	189	195													
13	1	78	88	116	144	154	170	176	182	188	200	209	214	225	234										
14	1	80	96	118	142	168	191	202	212	220	229	234	241	244	253	258									
15	1	73	80	94	117	144	170	193	212	220	227	233	238	241	244	246	247								
16	1	75	84	99	111	130	144	151	161	170	187	205	216	220	226	230	236	241							
17	2	77	92	106	129	146	164	176	191	204	215	221	226	231	237	241	245	252	256						
19	2	76	87	108	124	145	168	191	210	225	233	242	247	251	255	258	261	264	266	268	270				
20	2	76	89	102	121	145	164	179	202	217	226	236	242	246	249	252	255	257	259	261	263	265			
21	2	76	86	109	128	144	167	192	208	223	230	238	246	252	259	266	271	276	281	284	287	291	293		
23	1	73	96	131	140	153	162	172	178	184	197	211	222	236	244	251	265	268	273	277	279	281	282	284	285
Mean TL		75	88	108	127	145	161	176	189	201	213	222	233	239	245	250	254	260	267	272	275	279	288	284	285
SD		3	4	8	10	10	13	16	19	21	18	17	13	12	11	11	12	13	10	10	11	13	8		
Observed (direct readings)																									
Mean TL		84	96	119	129	160	176	183	188	187		202			241	264	259	254	257		265	269	275		293
SD		5	9	10	8	6	16	15	11	2									11		12	6	10		
n		15	6	16	11	5	4	4	5	3		1			11	1	1	1	2		2	2	2		1

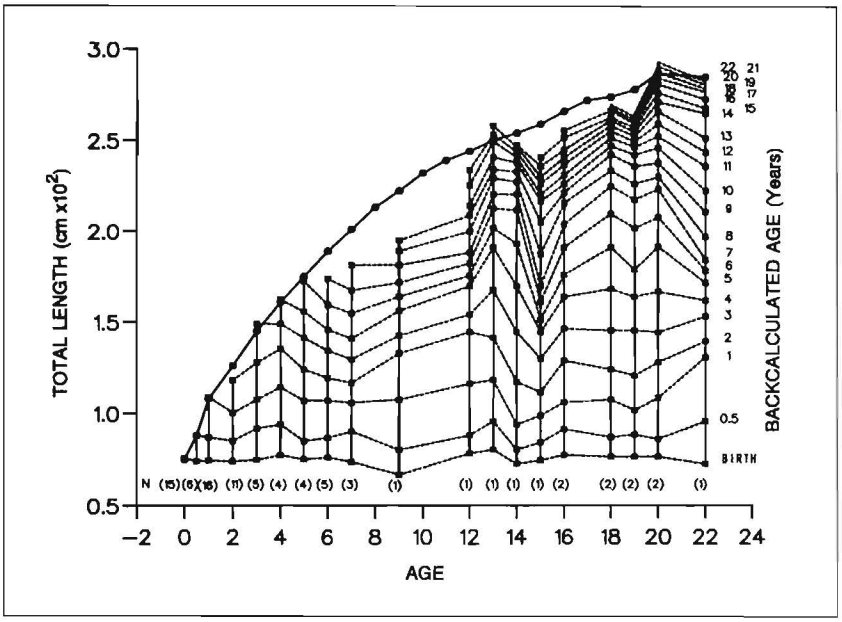

Figure 10

Variability of back-calculated mean lengths at age for silky shark. Circles are overall mean values. Boxes are back-calculated mean lengths at age obtained within cohorts, with numbers in parentheses indicating sample size (N) of each age class (solid lines). Broken lines interconnect the different values of length at age (corresponding age indicated in the right side of the graph) across cohorts. Some boxes on the upper right part of the graph are omitted for clarity.

Table 3

Von Bertalanffy Growth parameters for silky sharks from Yucatan obtained using the LFDA (Length Frequency Data Analysis) package. A partitioned analysis is based on multiple monthly LFD sets within a year. A summarized analysis is based on a single LFD set constructed by adding up monthly sets over time.

Type of analysis	Year	k	L_{inf} (cm TL)	t_0
Partitioned	1985	0.13	345	0.95
Partitioned	1986	0.115	325	0.97
Partitioned	1987	0.105	298	0.63
Partitioned	1988	0.085	313	0.22
Partitioned	1989	0.09	313	0.70
Summarized	1985	0.09	305	0.96
Summarized	1986	0.09	320	0.84
Summarized	1989	0.095	303	0.75
Summarized	All	0.115	365	0.86
Average		0.1016	320	0.76

(1984a) found *Carcharhinus falciformis* males 239 cm TL to be mature; contrastingly he noted mature females of only 216 cm TL. Additionally, Strasburg (1958) recorded gravid females of 213–236 cm TL in the Central Pacific, and Stevens (1984b) listed mature males at 214 cm TL and mature females at 202 and 208 cm TL for the southern Pacific (Tasman Sea).

Studies in the Atlantic more closely approximate our findings. For the eastern Atlantic, Bane (1966) and Cadenat and Blache (1981) provided lengths of 238–250 cm TL for mature females and 220 cm TL for mature males, roughly within the range of the present results. In the western North Atlantic, Springer (1960) reported a range of 68–84 cm TL for full-term embryos together with mature males from 221 cm and mature females from 233 cm. For the Gulf of Mexico, Branstetter (1987), with only six adult sharks, reported 215–220 cm as the range for male maturity and that females of 232–233 cm TL were mature. Size at birth and length for first maturity of females are roughly in accordance with our findings from the Campeche Bank. However, results from Springer (1960) and Branstetter (1987) suggest slightly smaller sizes at first maturity for males than those of ours. A possible explanation for these variations could be the different methods used for measuring length between their studies and ours.

More comprehensive research in the Gulf of Mexico may show females to have a size at maturity closer to that of the Indo-Pacific populations. On the other hand, it is possible for separate populations to have different characteristics.

Pratt (1979) found that the growth of claspers, testes, and epididymis of blue sharks is gradual and does not provide any clue to the approach of sexual maturity. Further, he determined that many male blue sharks, apparently fully mature when externally examined, lacked spermatophores and had small ductus defferentia and were thus not completely mature. Contrary to these findings, male silky sharks do have a well defined adolescence that extends approximately from 200 to 225 cm TL. The lack of internal examination of sharks in our study prevents verification of maturity derived from external features only. Further work will be needed to fully understand the onset of sexual maturity in male silky sharks.

The gestation time and birth season found here support Branstetter's (1987) suggestion of a 12–month late-spring-based cycle for development of *Carcharhinus falciformis* embryos in the Gulf of Mexico. Our findings are in contrast with Strasburg (1958), Fourmanoir (1961), Stevens (1984b),and Stevens and McLoughlin (1991), who noted an absence of a defined seasonality for reproduction in the Indian and Pacific Ocean populations. Although Strasburg (1958) does not present raw data, his analysis of 12 litters points towards a true difference in seasonality of reproduction between Gulf of Mexico and central Pacific populations. Based on these observations, Branstetter (1990) suggested silky shark populations might lack seasonal gestation periods in tropical areas; however, the Campeche Bank population has a seasonal gestation period and occupies in a tropical area. Furthermore, the populations studied by Bass et al. (1973) and Stevens (1984, a and b), and Stevens and McLoughlin (1991) all share roughly the same temperature ranges of the Gulf of Mexico but do not show a seasonal gestation period. Although available data are limited, there may be true differences among geographic populations. Estimation of the span of the total reproductive cycle in the females (i.e., if they give birth every year, or every other year) is also poorly known and should also be considered for future work. Branstetter (1987) gives the only available observations suggesting the entire cycle may take two years.

Age and Growth

Annuli, and growth bands, were readily discernible in silky shark vertebral centra. The poor resolution of bands on thin sections of vertebrae stained with silver nitrate was explained by Brown and Gruber (1988), who found that silver nitrate crystals formed in the sections and obscured the resolution needed for detailed studies.

The choice of December 30 for the date of annulus formation is only a preliminary estimate, as marginal increments appeared to decrease from August to November, and small sample sizes during this period prevented conclusive evidence. Branstetter (1987) reached the same conclusion for an early winter annulus formation for silkies in a nearby area but also suffered from few autumn data. More samples from the months of September to January are needed to document more accurately the date of annulus formation for Gulf of Mexico silky sharks.

Back calculations of size at birth (75 cm TL) matched the reproductive data on size at birth (76 cm TL). The present value of L_{inf} = 311 cm TL is in agreement with the maximum lengths of silky sharks collected in the Campeche Bank, which are 308 cm and 314 cm TL for females and males respectively. Longevity of the species is expected to be more than the 22+ years found for the largest specimen aged in this study (a 293 cm TL female). Several vertebral samples of sharks >300 cm TL in our possession are still waiting to be processed.

Our results differ somewhat with those found by Branstetter (1987) in the Northwest Gulf of Mexico. His fit of the von Bertalanffy model produced parameter estimates with a larger k (0.153), and a lower asymptotic length (290.5 cm TL) than those of the Campeche Bank (k = 0.101; L_{inf} = 311 cm TL). Furthermore, mean lengths-at-age between studies do not match for most of the sample range; Branstetter's values are consistently larger than the ones reported here.

Various explanations could be given for the disagreements found in growth parameters (sample bias, method of fitting the VBGM, combination of both); still, the differences in lengths-at-age remain unexplained. The sample size of both studies were rather similar, but the size ranges differed. Most vertebrae used in Branstetter's study came from sharks between 100 and 210 cm TL, but in our case two major groups at 80–205 cm and 240–295 cm TL constituted most of the samples. This difference may have a considerable effect on the shape of the VBGC and thus on the parameters. One of the reasons for Branstetter's low L_{inf} value is the absence of really large sharks in his samples. His largest specimen (267 cm TL) at age 13 was younger than the four sharks 275–293 cm TL aged in our study. The inclusion of larger, older specimens in our vertebrae samples is translated into a higher value of L_{inf} and a corresponding lower k value. In fact Branstetter (p.170) noted that the substitution of a L_{inf} value of 325 cm TL (which is closer to that presented here) produced a k value of 0.11 for his data, more in agreement with our findings. Accordingly, this could be the reason behind our different VBGM parameters.

Several hypotheses can be drawn to explain the different lengths-at-age of silky sharks from the Campeche Bank and the Northwestern Gulf of Mexico. Either true variations exist, or more likely, something is producing

an artificial difference in growth analyses. An argument against the first possibility is the proximity of the sampling locations, making a single stock, or at least strongly intermixing stocks very likely. This in turn suggests the likelihood of similar growth rates. Furthermore, the fact that the faster growth was found in the northernmost site contradicts the theoretical relationship between latitude, temperature, metabolism, and a faster growing equatorial stock. Parsons (1987) found a similar situation of fast-growing northern bonnethead sharks, *Sphyrna tiburo* ,and slow-growing southern specimens in Florida. This suggests environmental factors other than mean temperature could be more determinant for shark growth.

The existence of two separate stocks with different growth parameters would explain the present situation, but this possibility needs to be studied through specific stock identification techniques, such as biochemical genetics, in order to be properly assessed. Defining the issue of single or multiple stocks for many shark species has direct and important implications on the management of these resources which are being increasingly exploited across the area. These populations are being quoted as a single stock without conclusive evidence (i.e., Branstetter, 1990; Hoff, 1990).

The assumption that there are no real differences in growth leads us to search for obscuring effects. Application of the same technique does not always assure the same results; variations in the interpretation of each individual reader can account for different results (Cailliet et al., 1990), and cross-reading samples has been shown to help locate and sometimes solve this problem (Tanaka et al., 1990). In both Gulf of Mexico studies, only one reader was used. Comparisons and cross reading of both samples might clarify this point. It is also possible that neither sample is sufficiently representative of the population. Branstetter's samples come mainly from offshore deep-water specimens fished as swordfish bycatch, while ours belong mainly to grouper and shark fisheries from the continental shelf. This implies that our samples for young sharks could be biased towards slow-growing specimens remaining inside the Campeche Bank, because the fast-growing individuals could move to a more pelagic existence in the edge of the continental shelf as suggested by Branstetter (1987; p.169–170). Meanwhile, the northwestern Gulf of Mexico samples would represent exactly the opposite picture with a bias towards fast-growing individuals which leave the grouper-grounds sooner than their slow-growing siblings from the same cohorts.

The variability in the parameter L_{inf} found from the results of the LFDA program is attributable to the sensitivity of this procedure to the differences in the various sets of data analyzed. Other direct studies of age and growth determination in sharks have used simple mode definition to support their findings (Pratt and Casey, 1983; Casey et al., 1985). However, those studies used results from vertebral aging to define the modes in the length-frequency distribution. Such analyses do not constitute independent evidence supporting the study of vertebrae. In contrast to this, the present use of methodologies such as that of Shepherd (1987) is independent of the direct determination of age and growth, thus it provides stronger verification.

Conclusions

The silky shark in the Campeche Bank has a 12-month gestation period, giving birth to 10–12 pups with average total length of 76 cm during late spring and early summer, possibly every two years. Sex ratios probably remain close to 1:1 during life. Both sexes attain late sexual maturity, males at 225 cm TL (=10 yr, ≈72% of max. length) and females between 232–246 cm TL (>12+ yr; ≈74–78% of max. length) or smaller. More research on maturation and reproduction needs to be done in this species.

Growth in the silky sharks of the Campeche Bank can be variable, but in general these fish are slow growing (k=0.101), reaching at least 22 years of age. For this species, the alizarin-red-S technique applied to thin sections of vertebrae is a better method for direct studies of age and growth than silver nitrate staining. Length-frequency data are a good way of providing additional estimates of growth to verify direct studies.

Some differences between results of age and growth studies of silky sharks in the northwestern Gulf of Mexico (k=0.15, L_{inf} = 291 cm TL) and the Campeche Bank (k=0.10, L_{inf} = 311 cm TL) have been identified here. This suggests that the two populations may be somewhat distinct. Genetic study of the species in the Gulf of Mexico is proposed as the way to clarify the status of these populations.

Management measures for *Carcharhinus falciformis* should first clarify the structure of Gulf of Mexico stock(s), and consider the life-history characteristics of slow growth, late maturation, and limited offspring, which point towards a very fragile resource. In all probability, local stocks of this species cannot support sustained heavy fishing pressure.

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Growth Characteristics and Estimates of Age at Maturity of Two Species of Skates (*Raja binoculata* and *Raja rhina*) from Monterey Bay, California

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ABSTRACT

Estimates of growth and age at first maturity were determined for 171 *Raja binoculata* (big skate) and 132 *R. rhina* (longnose skate) collected between 1980 and 1981 along the central California coast. Analyses of vertebral centrum edges by month of capture suggested that a translucent growth zone forms in winter and an opaque growth zone forms in summer for both species. Age estimates for *R. binoculata* (175 to 1607 mm TL) ranged between 0 and 12; those for *R. rhina* (303 to 1322 mm TL) ranged between ages 3 and 13. The logistic growth function (LGF) fit the length-at-age data for *R. binoculata* better than a von Bertalanffy growth function (VBGF). Theoretical asymptotic length (L_∞ =1678 mm TL) was slightly greater for females than that for males (L_∞ =1388 mm TL), although growth coefficients were similar (k=0.37 and 0.43, respectively). The VBGF provided the best fit for *R. rhina*; females had slightly higher theoretical asymptotic length (L_∞ =1069 mm TL) and lower coefficient (k=0.16) than males (L_∞ =952 mm TL, k=0.26). Age at reproductive maturity was estimated at age 8–11 for *R. binoculata* and age 6–9 for *R. rhina*.

Introduction

The order Rajiformes comprises over 350 species of demersal skates (Compagno et al., 1989). The relatively large size and abundance of some species make them suitable for commercial harvest (Steven, 1932; Frey, 1971; Brander, 1981; Talley, 1983). Skates off the California coast have been exploited for food since the early 1900's (Steven, 1932). Five species of skates inhabit the waters off California, and two are important to the commercial fishery: the big skate (*Raja binoculata*) and the longnose skate (*Raja rhina*) (Holts, 1988). *R. binoculata* is the largest species, growing to a length of 240 cm total length. *R. rhina* has a long snout and is considerably smaller than *R. binoculata*, with a total length of 137 cm. Both species range from Alaska to Baja California, Mexico. Most of the skates landed in California are bycatch from trawlers, trammel nets, and longlines. The pectoral fins (wings) are used in domestic ethnic markets, especially Oriental, Italian, and Yugoslavian (Talley, 1983). The skate fishery is restricted generally to the San Francisco and Monterey areas (Oliphant, 1979; Talley, 1983), and in recent years skate landings in California have fluctuated between 26 and 348 metric tons (t); the average landing for 1980–90 was 125 t.

Life-history information for most species of California skates is unavailable. Available information suggests that skates have relatively slow growth rates and low reproductive potentials. Thus, as with other elasmo-

branch stocks, they are vulnerable to over harvesting by commercial fisheries (Holden, 1977). This study was initiated to acquire baseline life-history information on *Raja binoculata* and *Raja rhina*, including growth rates, age at maturity, and age-specific fecundities.

Materials and Methods

Skates were collected from commercial trawl vessels that target bottom fish from Santa Cruz to Monterey in 1980–81. Total length (TL) and disk width (DW) were measured, and total lengths are used throughout this report. Weights were measured to the nearest kg using a spring scale. Designation of stage of maturity for males and females was based on established criteria from Smith and Merriner (1987). Sexual maturity of male skates was based on two criteria: an abrupt change in the relationship of clasper length to TL, associated with clasper hardening (Babel, 1967); and the occurrence of coiling in the vas deferens. Reproductive status of females was assessed on freshly caught specimens as 1) immature-ovaries, thin and of homogeneous cellular appearance throughout the gonad; 2) maturing-ovaries showing differentiation of ova, ova approximately 5 to 10 mm in diameter; and 3) mature-ovaries with large yolked eggs greater than 10 mm in diameter.

Age Determination

For age and growth analyses, the 10th through the 20th vertebral centra were removed from each skate and frozen. Initially, vertebral centra sections (*R. binoculata*, n=60, and *R. rhina*, n=30) were subsampled based on specimen size: small (<700 mm), medium (700–1000 mm), and large (>1000 mm).

For analysis, the connective tissue and the neural arch were removed from 3 or 4 centra from each fish. Centra were air dried, fixed in 70% ethanol for two to four hours, then placed in 100% ethanol for 48 to 72 hours to clarify the rings (Richards et al., 1963). Two centra were mounted individually on wood blocks and embedded in a medium of paraffin wax, calcium oxide powder, and decoloring carbon. A wafer section was cut from the center of the centra with a Bronwill high-speed sectioning machine. The thin sections (0.25–0.30 mm) were removed from the wax and rinsed in 95% ethanol. To clarify rings, a drop of mineral oil was placed on each section.

Two terms in this study are used to describe the patterns found on calcified centra: ring and annulus. The term "ring" describes depositional growth zones found on skate centra. Opaque rings are those with dense cells and high concentrations of calcium and phosphorus (Cailliet and Radtke, 1987); they appeared white when viewed with reflective light on a black background (Fig. 1). Translucent rings are less mineralized, and appear dark when viewed with reflective light (Fig. 1) as described by Chilton and Beamish (1982). The term "annulus" refers to each pair of translucent and opaque rings (Fig. 1). Rings in sections were counted twice by the senior author with the aid of a dissecting microscope at a magnification of 20× under reflective light. Centra were read by an additional reader to determine inter-reader variability. The variability between the two readings was assessed by calculating the average percent error (APE) (Beamish and Fournier, 1981), and percent error (D), an alternate index of precision proposed by Chang (1982). If both readers disagreed in their assignment of the number of annuli, additional readings (3 or 4) were made until agreement within one to three years was obtained. Data for a centrum were discarded if agreement was not reached.

Centrum diameter (CD) was measured four times with an Olympus II-C Image Analyzer and dissecting microscope. An average of the four measurements was plotted against TL, and the relationship between CD and TL was described by linear regression (Martin and Cailliet, 1988). Centrum edge characteristics (i.e., opaque or translucent) were plotted against month of capture to detect trends in deposition.

Growth curves were fitted for both sexes combined and independently by using the von Bertalanffy growth equation (VBGE):

$$L_t = L_\infty [1 - e^{-k(t - t_0)}]$$

where L_t = total length at time t
L_∞ = maximum theoretical length
k = growth coefficient

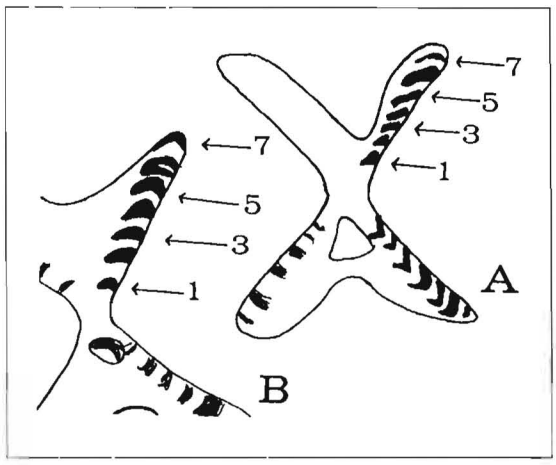

Figure 1
Longitudinal cross sections of a vertebral centrum of (**A**) *Raja binoculata* and (**B**) *Raja rhina*. Arrows show 7 broad translucent and narrow opaque ring pairs on each section.

t_0 = theoretical age at zero length.

Additionally, data were fit to the logistic growth equation:

$$Y(t) = K/\{1+[(K- Y^0)/Y^0]\ [\exp(-rt)]\}$$

where Y_t = Length at time (age) t
K = Asymptotic length
r = logistic growth coefficient
Y_0 = size at birth.

Both equations were fit using a software program, FISHPARM (Prager et al., 1987).

Results

Maturity

Raja binoculata—Between January 1980 and September 1981, 171 *Raja binoculata* were captured from Monterey Bay: 103 males (175 to 1321 mm) and 68 females (227 to 1607 mm). *R. binoculata* were captured in all months except November and December. The relationship between TL (mm) and weight (kg) was significant and curvilinear (Fig. 2).

Males appear to mature at 1000–1100 mm (Fig. 3). Males (n=38) less than 782 mm had straight vas deferens, and were staged as immature. Twenty-nine specimens (782–1086 mm) showed moderate coiling of the vas deferens, and were staged as maturing. All males larger than 1086 mm were staged as fully mature.

The analysis of maturity stages indicates that female *R. binoculata* mature at sizes greater than 1300 mm (Fig. 4). Immature females ranged from 200 to 1300 mm, and maturing specimens between 500 and 1200 mm. Specimens larger than 1300 mm were staged as mature.

Raja rhina—Between January 1980 and August 1981, 132 *Raja rhina* were captured from Monterey Bay: 64 males (359 to 1322 mm) and 68 females (303 to 1068 mm). *R. rhina* were captured during seven months, excluding May, June, September, November, and December. The relationship between TL (mm) and weight (kg) was significant and curvilinear (Fig. 5).

Males become sexually mature at 615–740 mm (Fig. 6). Males smaller than 615 mm (n=17) had straight vas deferens and were immature. Twenty-two specimens (615–740 mm), showed moderate coiling of the vas deferens and were staged as maturing. All *Raja rhina* larger than 740 mm were sexually mature.

Our analysis of the maturity stages indicates that female *R. rhina* may become sexually mature at 700 mm (Fig. 7). Although females ranging between 300 and 900 mm were immature, those between 600 and 1000 mm were maturing. All females >1000 mm were staged as sexually mature.

Age Analysis

Centrum Relationship—The centrum diameter of *R. binoculata* increased in a significant and linear fashion with TL (mm) (CD=0.29+0.008 TL, R^2=0.93: Fig 8). The translucent rings were much broader than the opaque rings (Fig. 1A). The relationship between TL (mm) and CD (mm) for both sexes combined was

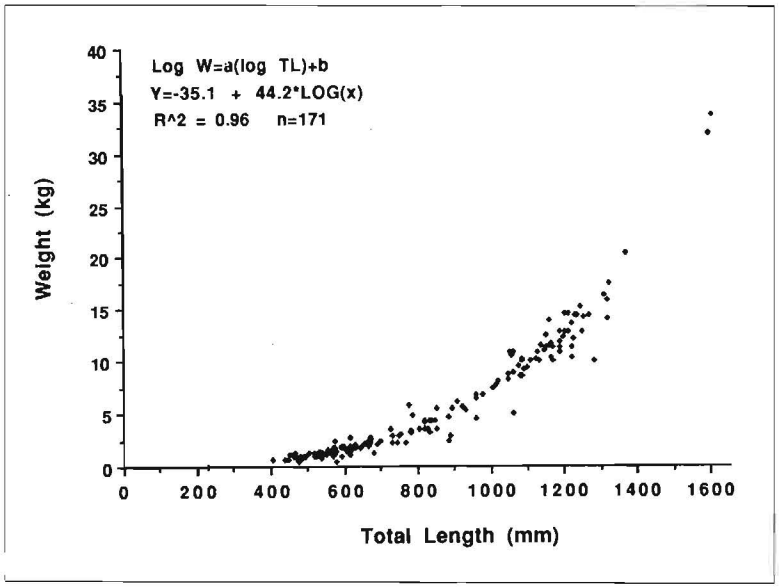

Figure 2
Relationship of weight and total length for both male and female *Raja binoculata* used in this study.

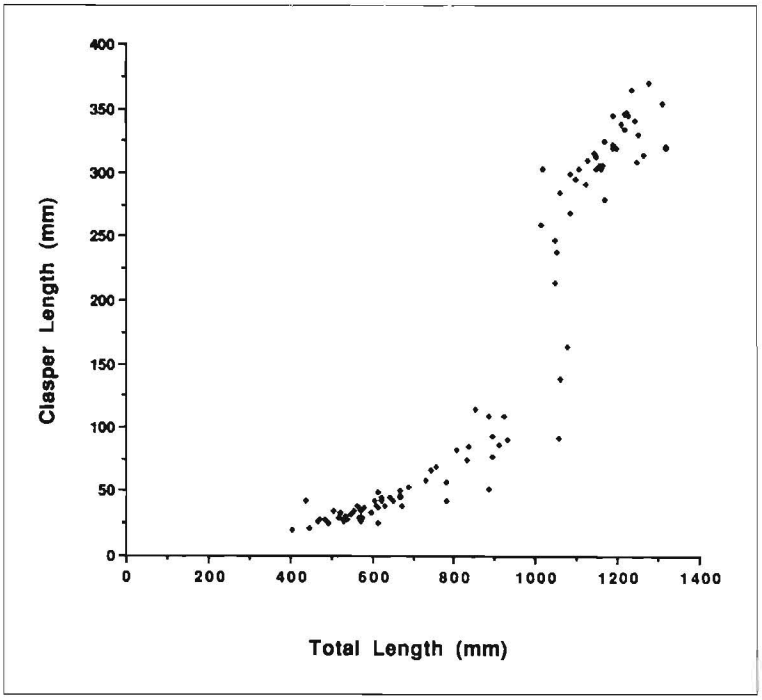

Figure 3
The relationship between total length and inner clasper length of 103 male *Raja binoculata*.

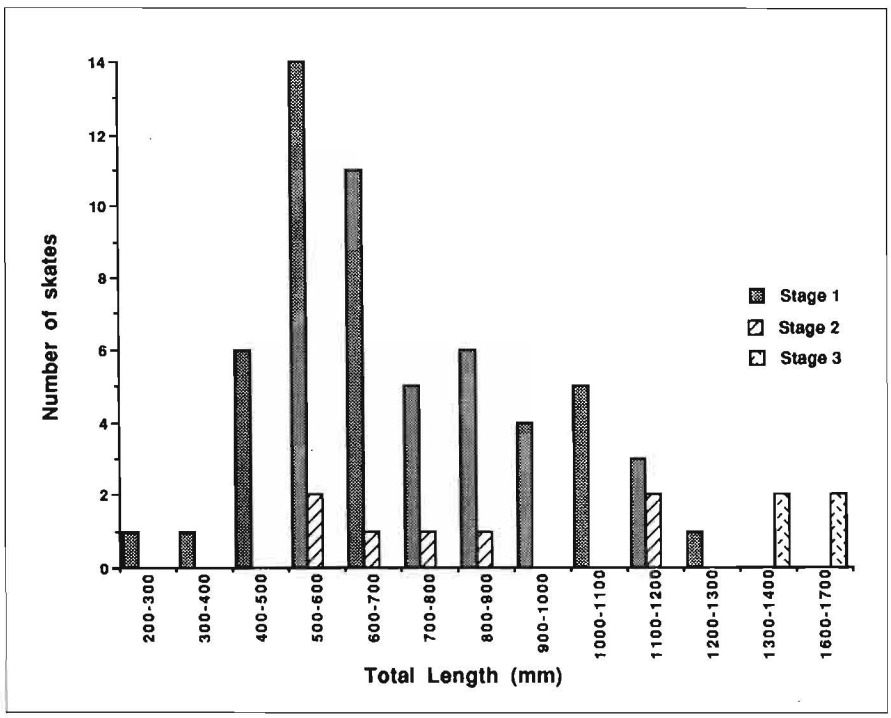

Figure 4
A histogram of stages of maturity in 169 female *Raja binoculata*. Stage 1: Immature, Stage 2: Maturing, and Stage 3: Mature.

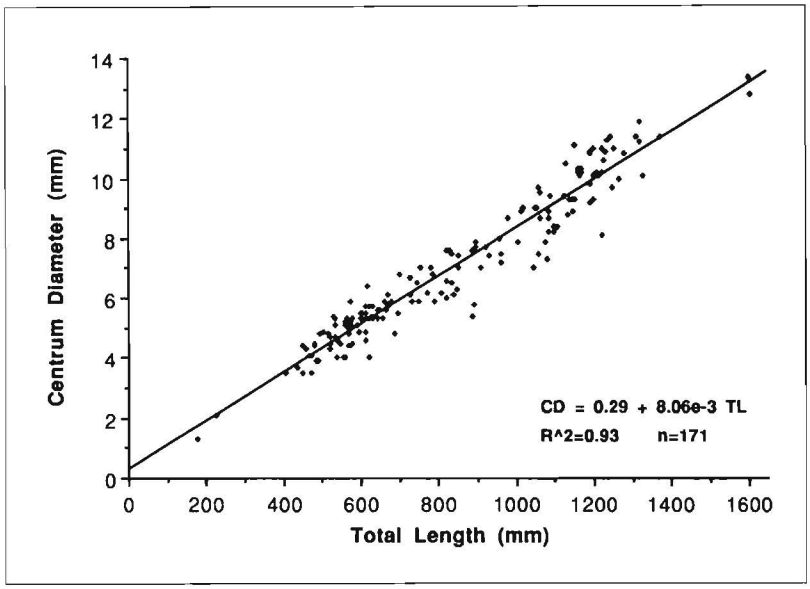

Figure 5
Relationship of weight and total length for both male and female *Raja rhina* used in this study.

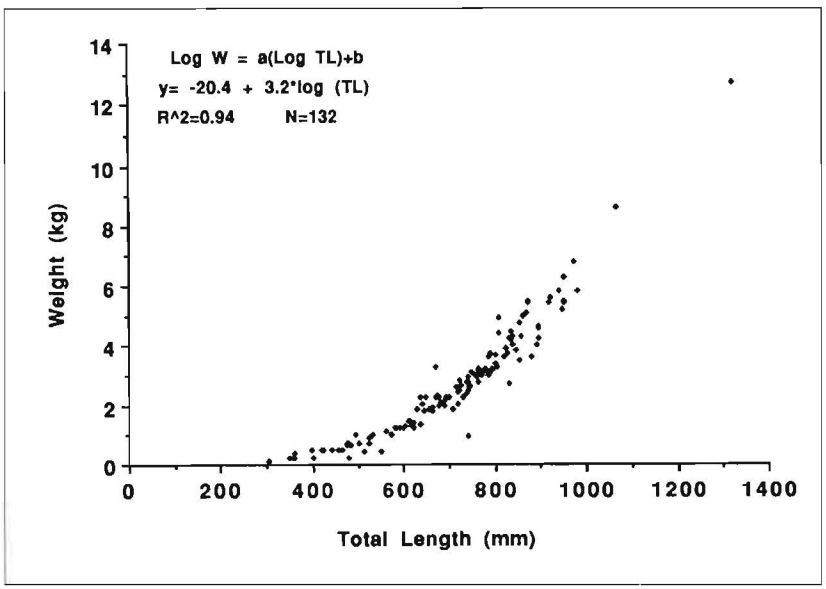

Figure 6
The relationship between total length and inner clasper length of 64 male *Raja rhina*.

significant and linear in *Raja rhina*:(CD=0.31+0.0084 TL, R^2 =0.83: Fig. 9).

Precision Analysis—Results of the precision analyses are summarized in Figures 10 and 11 for *Raja binoculata* and *R. rhina*, respectively. Average percent error (APE) and percent error (D) associated with the senior author's readings were 5% and 4%, respectively, for the former, and 4% and 3% for the latter species. Precision of age estimates between readers was relatively good and high percentages of agreement were calculated in all size classes of each species. For *R. binoculata*, 95% of the small, 100% of the medium, and 90% of the large fish had age estimates that agreed within 2 years. For *R. rhina*, 100% of the samples had counts that agreed within 2 years.

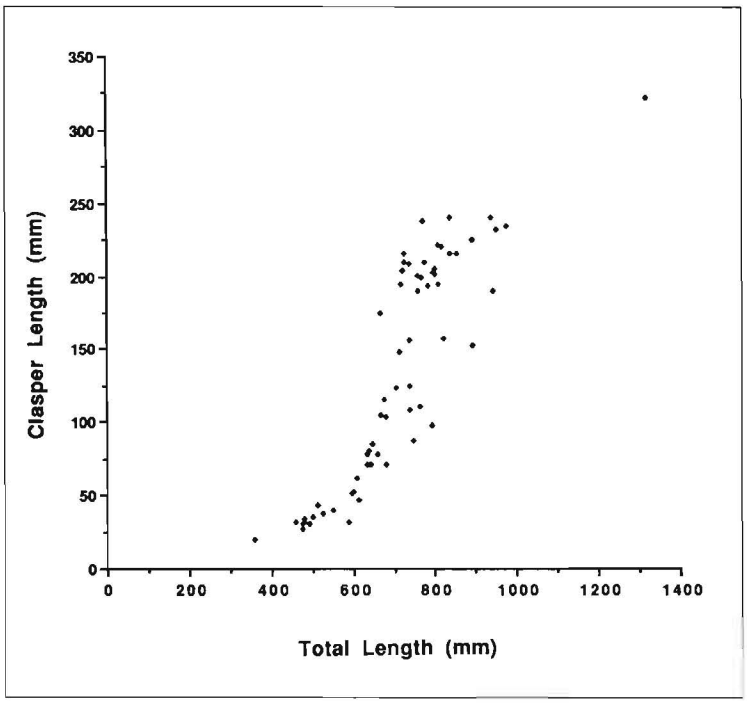

Figure 7
A histogram of stages of maturity in 68 female *Raja rhina*. Stage 1: Immature, Stage 2: Maturing, and Stage 3: Mature.

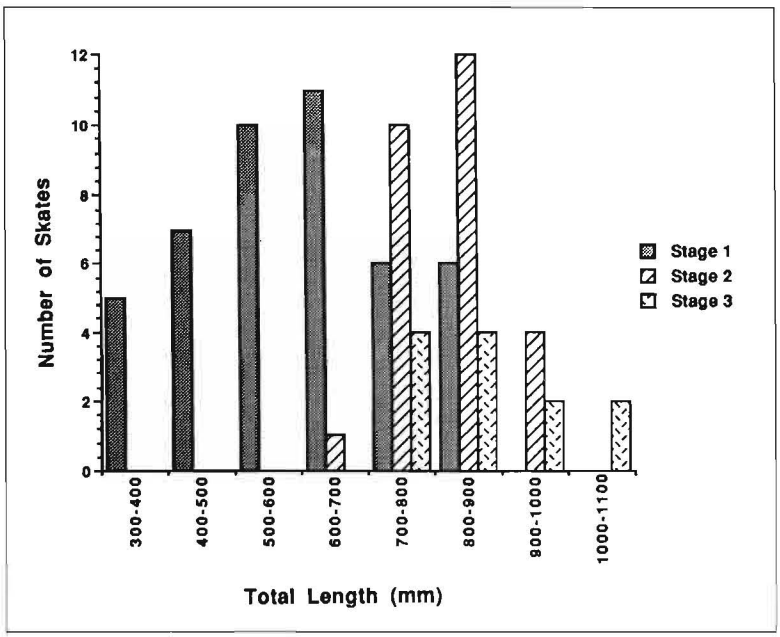

Figure 8
Relationship between total lenght and centrum diameter (CD) for both male and female *Raja binoculata* used in this study.

Edge Analysis—Opaque rings occurred mostly in summer and translucent rings in winter on vertebrae of *R. binoculata* (Fig. 12), although some translucent edges were seen in specimens captured in all months sampled. Two skates, assumed to be young-of-the-year, could not be characterized.

Centrum edges of *Raja rhina* provided little evidence of seasonal ring deposition (Fig. 13). It appears that

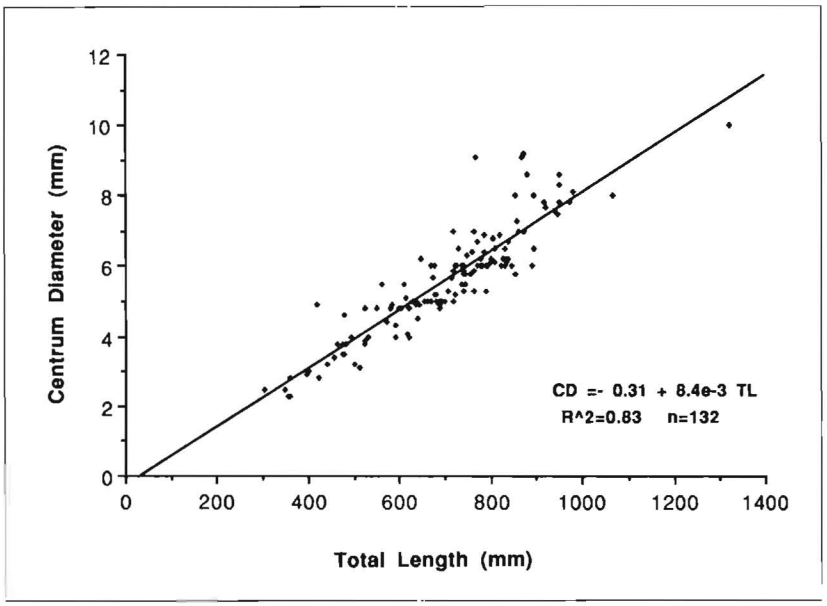

Figure 9
Relationship between total length and centrum diameter for both male and female *Raja rhina* used in this study.

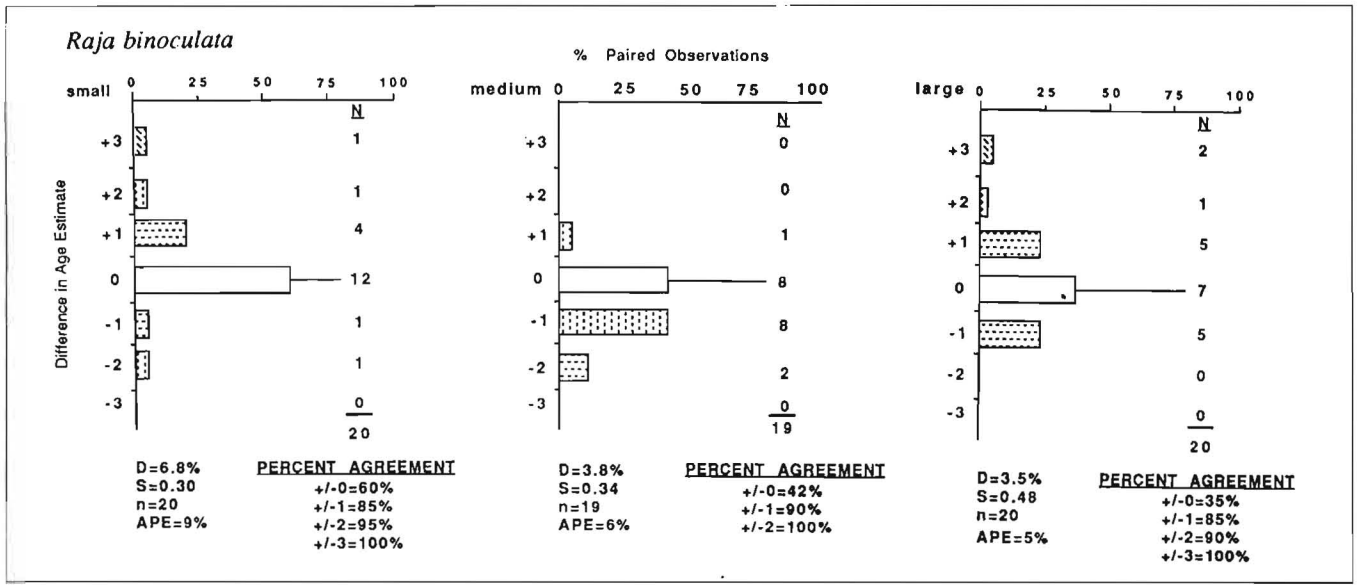

Figure 10
Precision of age determination of *Raja binoculata*. Histograms represent the difference (as the percentage of paired band counts by 0, 1, 2, and 3 years) between the two readers. The proportions of counts which agreed within a certain number of band counts are listed under "percent agreement," the symbols D, S, *n*, and APE represent Beamish and Fournier's (1981) and Chang's (1982) percent error, standard deviation, number of centra (sample size) and average percent error, respectively. *N* is the number of centra for that age estimate.

translucent rings form in the winter and opaque ones in summer. Opaque edges were found in specimens from January through August, while translucent edges were found during all months.

Age Determination

Male *Raja binoculata* that were staged as immature were estimated to be age 5 or younger. Fully mature males

were estimated to be age 10–11, mature females were estimated to be age 12. *Raja rhina* males that were estimated to be immature were aged 6 years or less. Maturing males were approximately age 7 and mature individuals were estimated to be age 10–11. Female *R. rhina* that were sexually mature were estimated to be age 10–12.

The logistic growth curve fit the size-at-age estimates best for *Raja binoculata* with smaller standard errors than the VBGF for males, females, and both sexes combined (Fig. 14). Males ranged between age 0 (175 mm) to age 11 (1321 mm). Females ranged between age 0 (227 mm) and age 12 (1607 mm). Age 1–2 males and females were unavailable to us. There appeared to be no substantial difference in growth parameters between males and females.

The von Bertalanffy growth function provided a reasonable fit, with low standard errors, to the length-at-

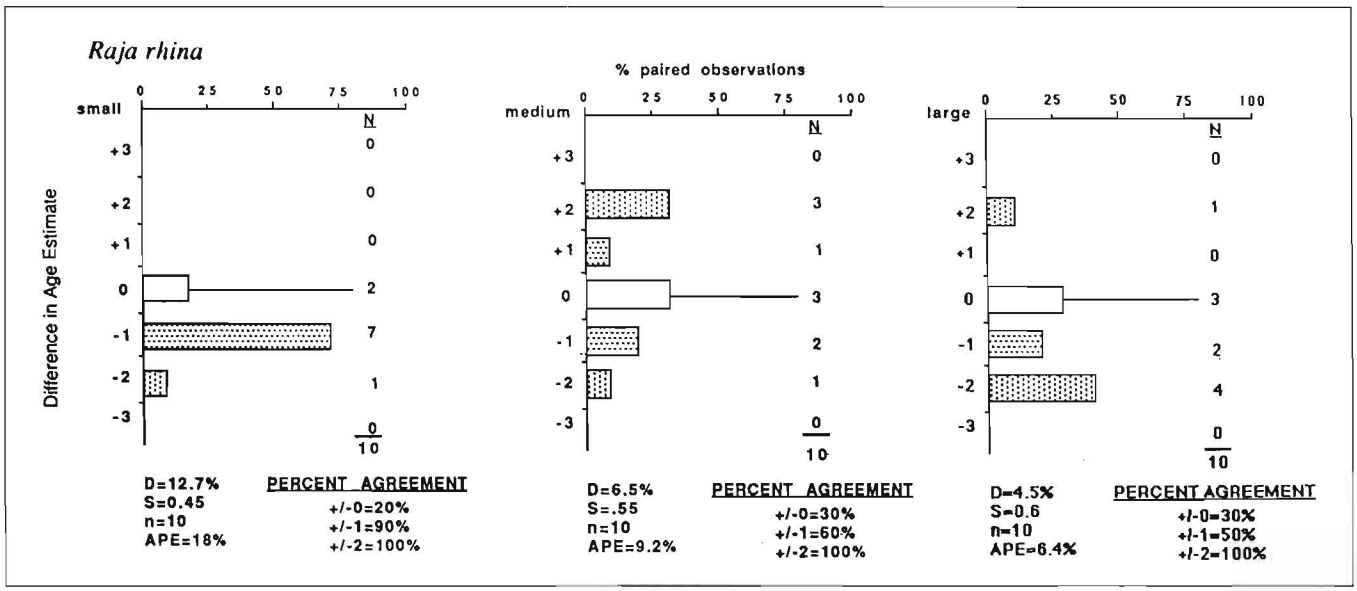

Figure 11
Precision of age determination of *Raja rhina*. Details as explained in Figure 10.

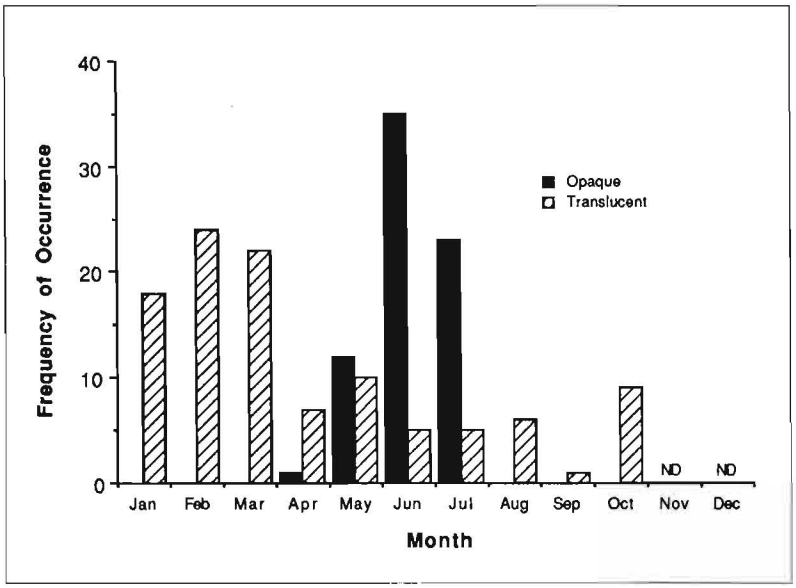

Figure 12
Seasonal changes in centrum edge characteristics of *Raja binoculata*. ND=no data.

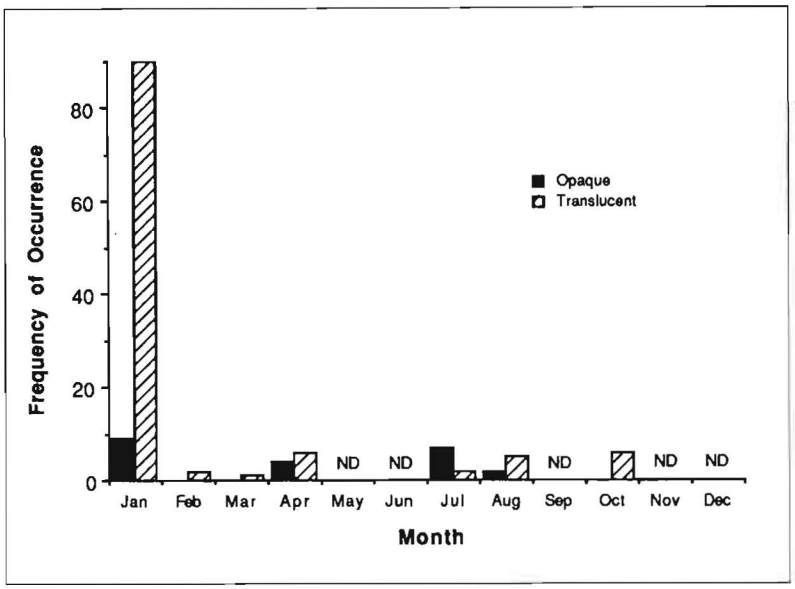

Figure 13
Seasonal changes in centrum edge characteristics of *Raja rhina*. ND=no data.

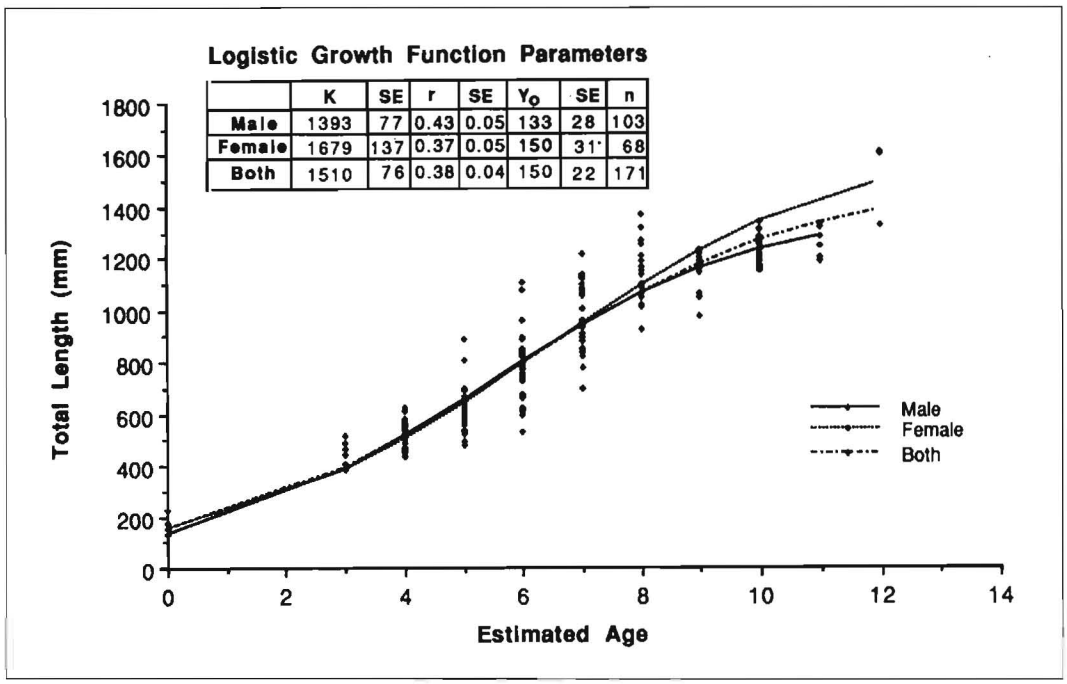

Figure 14
The logistic growth curve for male, female and both sexes combined of *Raja binoculata*.

age data for *R. rhina* for males, females and both sexes combined (Fig. 15). Males ranged between age 3 (359 mm) and age 13 (1322 mm). Age 0–2 males were absent from our collections. Females ranged between age 2 (303 mm) and age 12 (1086 mm), and age 0 and 1 females were unavailable to us. There appeared to be no substantial difference in the growth parameters between males and females.

Discussion

Determination of sexual maturity in male elasmobranchs is most frequently observed by changes in relative size, and hardness and development of claspers (Pratt, 1988). Skates exhibit an abrupt transition in clasper total-length relationship upon sexual maturity, similar to other batiods (Smith and Merriner, 1987). Based on

these two factors, the onset of male sexual maturity of *Raja binoculata* occurs between age 7 and 8 (1000–1100 mm), which is 57–72% of the calculated asymptotic TL. Similarly, male sexual maturity of *Raja rhina* occurs at age 5 (600 mm), which is 62% of the asymptotic total length.

Considerable discrepancies exist in the literature concerning the size and age of female skates at sexual maturity. Holden (1972) and DuBuit (1983) estimated that the *Raja* spp. in their studies reached reproductive maturity at estimated ages of 9–12 years. Observations on reproductive maturity of female *Raja binoculata* suggest that maturity is attained at age 12 (1300 mm), which represents 82% of their asymptotic total length found in this study. For female *R. rhina*, maturity is attained at age 8 (700 mm), which is 66% of the asymptotic total length. We may have misjudged *R. binoculata* females at 500–600 mm as maturing, since sexual maturity was not attained until 1300 mm. More reproductive studies need to be done on female *Raja binoculata* to gain a better understanding of maturity stages. Thus, the two species of skates examines in this study were reproductively mature at 50% of their estimated maximum total length.

Good readability of the growth zones on the centra of both species led to good agreement between the two readers. For the size range of these species, percent errors ranged from high values (6.8 and 12.7) for the smaller skates to lower values (3.5 to 6.5) for medium and large skates. This translates to a potential error for the 0–3 year old, where the margin of the first ring may have been misinterpreted.

Vertebral ring formation for *Raja binoculata* and *Raja rhina* probably provides a continuous record of growth. This is supported by data showing that increases in total length are accompanied by increases in centrum diameter; also the formation of paired opaque and translucent rings in vertebrae appear to have a seasonal periodicity. Therefore, we concluded that one opaque-translucent ring pair represented one year of growth.

For *Raja binoculata*, translucent bands form most frequently in winter and opaque bands in summer. The translucent rings were broader than the opaque rings and thus suggest greater growth in winter. In other skate species, such as, *Raja fusca* (Ishiyama, 1951), *Raja hollandi* (Ishiyama, 1951), *Raja erinacea* (Waring, 1984), *Raja clavata* (Holden and Vince, 1973), and *Raja montagui* (Ryland and Ajayi, 1984), the seasonal formation of opaque rings has been associated with rapid summer growth periods and translucent rings with slow winter growth. Centrum edges of *Raja rhina* showed little evidence of seasonal ring deposition, although translucent edges predominated in winter and opaque edges often formed in summer. A larger sample size

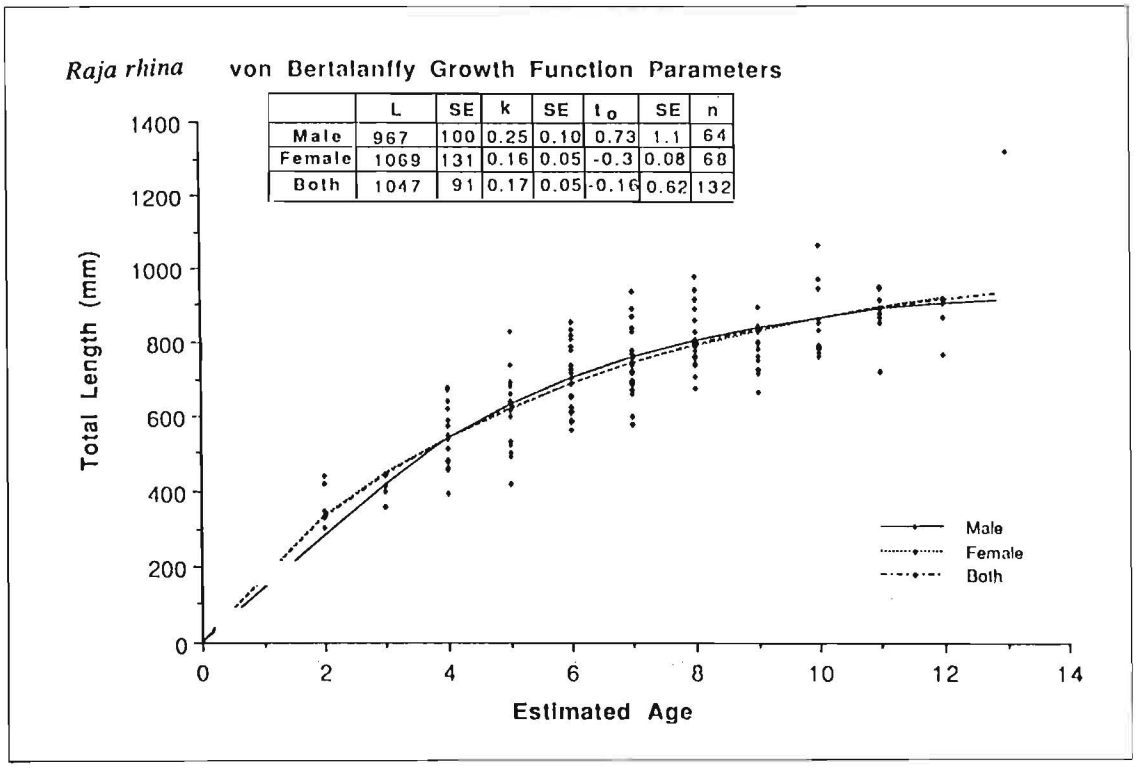

Figure 15
Von Bertalanffy growth curve for male, female, and both sexes combined of *Raja rhina*.

from each calendar month would probably better define the season of zonal deposition.

Factors that mediate the temporal periodicity of calcium deposition in elasmobranch centra are not known. Changes in temperature, salinity, light, and diet (Stevens, 1975), and stress-related activities such as migration (Pratt and Casey, 1983) have been suggested. For *Raja binoculata* and *R. rhina*, changes in the diet from low calcium when young to an increased calcium-rich diet when older[1], and an unloading of calcium from the plasma to the vertebrae associated with inshore migrations, or both, may be responsible for the opaque bands being deposited. Opaque edges were found in specimens captured inshore in the summer. Similarly, movement in and out of shallow water at all times of the year, and associated temperature and salinity differences may be responsible for the translucent edge found in all sample months.

The von Bertalanffy growth equation for *Raja binoculata* overestimated L_∞ for the females and underestimated the L_∞ for both sexes combined. Growth in length as shown in the logistic growth curve *R. binoculata* (Fig. 14) is fastest during the third to eighth year for males and third to tenth year for females and decreases thereafter. Females grow slower (r=0.37) yet reach a larger size (L_∞ =1679 mm) than the males (r=0.43; L_∞ =1393 mm). The growth parameters for males and females are not substantially different. The estimated asymptotic length (1510 mm) for combined sexes approximates the maximum length observed during the study (1607 mm), but underestimates the maximum reported in the literature, 2400 mm (8 feet) (Eschmeyer et al., 1983). This may be due to the limited data points for older individuals.

The growth parameters generated from the von Bertalanffy growth equation for *Raja rhina* indicate that growth is similar for both sexes (Fig. 15). However in both cases, the calculated asymptotic lengths for *Raja rhina* were smaller than the reported size for this species. The largest specimen in our study was 1322 mm, whereas the reported maximum size in the literature is 1370 mm (Miller and Lea, 1972). Calculations of L_∞ for both sexes (1047 mm) combined underestimates the maximum length (1322 mm) observed during this study and in the literature.

The growth coefficient values for *Raja binoculata* and *Raja rhina* are comparable to those reported in the literature for other skates (Holden and Vince, 1973; Waring, 1984). A comparison of the growth coefficient values from both species shows that *Raja binoculata* has a faster growth rate than *Raja rhina* and attains its asymptotic length sooner.

One must consider sample size and biases when obtaining specimens. In this study, even though the sample sizes were relatively small, the biases were real but unavoidable because specimens for these two species were obtained from commercial fishing vessels. Owing to gear selection and marketable size, a narrow size range was taken. Thus the smaller and larger size classes were underrepresented which led to underestimated L_∞ in the growth equations for both species of skates.

The age of the oldest *Raja rhina* (13, TL=1322 mm; Fig. 14) may be overestimated. False rings (rings which do not completely encircle the centra) may have been counted on this specimen, thus increasing the age estimates. Richards et al., (1963) occasionally saw false rings in the centra of *Raja eglanteria*. Waring (1984) observed checks (false rings) in *Raja erinacea* and speculated that these checks formed in response to physiological stress.

Some difficulty was encountered in estimating the age of *Raja binoculata* and *Raja rhina* because of the appearance of the first and last ring formation. Daiber (1960) and Richards et al. (1963) experienced difficulty interpreting the first ring, which varied in width depending on whether the skate was born in the spring or autumn. Brander and Palmer (1985) reported difficulties interpreting the "nucleus," the first ring, and therefore a consistent birth date for their study. In this study, centra with four to eight annuli were the easiest to read, but we found it difficult to distinguish the rings of the younger (0–3) and older (9–12) skates. Brander and Palmer (1985) stated that when growth is reduced because of food limitations, environmental conditions, or other causes, the appearance of an annulus may change; they suggested that the method of age determination may require modification.

Only by validating the growth zones can age estimates for either of these species of skates be established confidently (Beamish and McFarlane, 1983; Cailliet, 1990). Validation techniques suggested by Cailliet et al. (1986) such as laboratory grow outs, tag-recapture, and perhaps oxytetracycline labeling alone could be used in future studies to validate the age estimates for these species.

Holden (1977) questioned the idea of sustainable fisheries for elasmobranchs, basing his conclusion on the linear relationship between stock and recruitment for most elasmobranchs. According to Holts (1988), elasmobranchs are so vulnerable to over-exploitation that certain populations may continue to decline for some time even if fishing pressures were removed immediately.

Skate landings as reported in the U.S. at present are incomplete and various species are seldom distinguished

[1] Badkin, R. 1990. Food habits of two size groups of the big skate (*Raja binoculata*) occurring off the Central California Coast. Student paper. Moss Landing Marine Lab., P.O. Box 450, Moss Landing, CA 95390.

(Frey, 1971; Brander, 1981; Talley, 1983); therefore, it is difficult to detect fluctuations in stock size. Theoretically, guidelines to prevent over-exploitation should be established if a sustainable fishery is developed for skates on the Pacific Coast of the U.S. At present, however, skates remain a bycatch of trawl fisheries for other demersal species. Martin and Cailliet (1988) suggest that the size of a population and regulatory size limits would have to be established, providing the non-reproductive individuals an opportunity to mature and reproduce. This study has provided at least minimal estimates of various life history parameters, should either species of skate in the future come under the scrutiny of fisheries management agencies.

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